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Lund 1981

ENVIRONMENTS AND CO-EXISTENCE OF IDOTEA SPECIES
IN THE SOUTHERN BALTIC

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B. Sc., Ld

DOCTORAL DISSERTATION

BY DUE PERMISSION OF THE FACULTY OF SCIENCE AT THE
UNIVERSITY OF LUND TO BE PUBLICLY DEFENDED AT THE
DEPARTMENT OF ANIMAL ECOLOGY, ECOLOGY BUILDING,
HELGONAVÄGEN 5, LUND, SWEDEN, ON FRIDAY 15 MAY, 1981,
AT 01.15 P.M. FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

LUND 1981

THE THESIS WILL BE DEFENDED IN ENGLISH.



This thesis is based on the following papers:

- A. Idotea in the southern Baltic; distribution and environmental factors.
- B. Life history and fecundity differences in Idotea baltica, I. granulosa and I. chelipes in the southern Baltic.
- C. Food and substrate preference of three co-existing species of Idotea (Crustacea, Isopoda). A laboratory investigation.
- D. Colour polymorphism in Idotea baltica (Crustacea, Isopoda) in the southern Baltic.
- E. Predation on polymorphic Idotea baltica (Crustacea, Isopoda) by Zoarces viviparus (Teleostei, Zoarcidae) - a laboratory study.

In the following they will be referred to by their respective letters.

1. Introduction

The isopods Idotea baltica (Pallas), I. chelipes (Pallas) and I. granulosa (Rathke) are mainly littoral or sublittoral forms commonly occurring on algae. Their distribution extends from the Baltic Sea (Segerstråle 1944, 1969, Sywula 1964, Muus 1967), to the British Isles (Howes 1939, Naylor 1955), and France (Labourg 1971) and I. baltica has been reported from the Mediterranean and the Black Sea (Collinge 1917). The group consists of both free-living and parasitic (ecto- and endoparasitic) species. The economic aspect of the ectoparasitic species are reported in the fish and timber industries (Kjennerud 1950, Naylor 1972). They are found as pests on fishes causing serious damage to the live catches in nets, and wood boring species are reported to have caused considerable economic losses in the United States (Naylor 1972).

2. Study area

The Baltic Sea is sometimes described as the World's largest estuary. It is connected to more saline areas through the Belts and the Sound. The water masses are divided into two layers; a surface layer with lower salinity as a result of a large freshwater supply from run off and precipitation and a deep water layer originating from the North Sea with higher salinity. The average salinity of the surface layer is about 7.5 ‰. With a good water movement, oxygen is not a limiting factor (Kinne 1970).

The Falsterbo peninsula is located where the Baltic Sea meets the more saline water of the Sound. The peninsula projects westwards and is on the border between watermasses of slightly different chemistry. Thus, on the northern side of the Falsterbo peninsula the water is somewhat more saline than on the southern side.

The three isopods Idotea baltica, I. chelipes and I. granulosa all occur in the coastal waters of the Falsterbo peninsula. The gradient of water salinity and different degree of exposure between localities on the northern and southern side of this peninsula, provide excellent opportunities to study the ecological requirements of these three species.

One of the localities (loc. A) is situated in a sheltered bay on the northern side. Here the salinity and temperature were high while the more exposed localities (locs C - E) on the southern side were all somewhat cooler with more brackish water of higher oxygen content. In spring, however, the salinity in loc. A dropped below the values of all the other localities. This was due to the inflow of freshwater into the sheltered bay at the time of ice melt.

Southeasterly winds dominated in all the localities for most of the time. During summer and autumn the prevailing wind direction was westerly while easterly winds dominated during winter and spring. Low water levels prevailed mostly during the winter and spring whereas the water level was higher during the summer and autumn.

3. Factors affecting the distribution of the Idotea species in the southern Baltic (paper A)

The distribution of the Idotea species is influenced by many environmental factors, including salinity, temperature and water movements. The influence of one factor cannot be totally isolated from the rest as they often interact. I. baltica and I. chelipes

from the rest as they often interact. I. baltica and I. chelipes occurred in about similar abundances while I. granulosa was scarce. This last species was absent from the most sheltered locality (loc. A) and virtually absent from locality B, both on the northern side of the peninsula. In these two localities I. chelipes made up over 75 % of the isopods. I. baltica dominated in the more exposed localities on the southern side. Here I. granulosa also was found but always in relatively low numbers. In experiments, the isopods' tolerance to water of low salinity was studied. I. chelipes was found to be the most tolerant and I. granulosa the least tolerant to water of low salinity. The fact that I. granulosa was nearly absent from the northern, more saline, side can probably be ascribed to the pronounced drop in salinity during spring in these waters.

4. Life history differences (paper B)

Idotea baltica and I. chelipes had rather similar life cycles with a breeding season beginning in May. During the summer months at least two juvenile cohorts were produced after which the old generation died. Some early born females possibly produced a second generation before the winter. The bigger I. baltica female carried maximum 138 eggs while the much smaller I. chelipes had a maximum of 95 eggs. These two species' distinctly different size is suggested to facilitate their co-existence and close agreement regarding reproduction. I. granulosa, however, being of nearly similar size as I. baltica produced only one cohort. I. granulosa started breeding one month earlier than the other two. Maximum number of eggs found in I. granulosa was 116. The relative fecundity (No. of eggs per equal-sized female) was highest in I. chelipes (54 eggs / ♀) and lowest in I. baltica (40 eggs / ♀). It was observed that females generally carried fewer embryos than eggs in the marsupia. Fungi infecting the eggs were responsible for this egg mortality. Large proportions of the females of all species were found with eggs infected by fungi. I. baltica was the most heavily infected.

5. Preference of Idotea for algal food and shelter (paper C)

A certain isopod's preference for a specific algal species may be influenced by the alga's stage of development (Naylor 1955, Jansson 1967) and its sensory, nutritional and mechanical properties (Westoby 1974).

In a laboratory experiment the three isopod species were presented different algal species. These included Fucus, Cladophora, Enteromorpha, Chorda and Ulva and the phanerogam Ruppia. In single-species experiments, all isopod species showed highest preference for Ruppia. This preference was maintained by both I. baltica and I. chelipes also when they were studied in combination with the other two species. I. granulosa, however, shifted its preference from Ruppia to Chorda when together with I. baltica and to Fucus when together with I. chelipes. This is taken as evidence for the lower competitive ability of I. granulosa compared to the other two species.

6. Colour polymorphism in Idotea baltica (paper D)

Six different phenotypes of I. baltica were recorded. These were all found in all localities. The phenotypes were either uniformly coloured (uniformis) in green, brown or black and they had a more mottled appearance (albafusca, bilineata, lineata, maculata, pseudolineata). Uniformis was by far the most common phenotype and lineata the least common. With the exception of albafusca all the other phenotypes had more males than females.

The phenotypic diversity in a certain locality correlated with the diversity of the algal community. It was also apparent that green morphs of uniformis dominated where green algae were frequent and brown morphs where brown algae were common. The more mottled phenotypes (bilineata, maculata, pseudolineata) were frequent in the more exposed localities where the environment was more heterogeneous.

7. Predation on the polymorphic species Idotea baltica (paper E)

Differential predation on selected phenotypes of I. baltica was studied in the laboratory. Different algal species was provided as background and shelter for the isopods. Zoarces viviparus, a fish common in the coastal waters of the Falsterbo peninsula was used as a predator. It was shown that phenotypes that matched well with the background were taken in lower numbers than others. It is suggested that the observed distributional patterns of phenotypes of Idotea baltica around the Falsterbo peninsula was a result of differential predation on the morphs.

Acknowledgements

I wish to thank Prof. Per Brinck for his criticism, encouragement, stimulating discussions and facilities at the Department of Animal Ecology, University of Lund. Drs Bo W. Svensson, Lars M. Nilsson, Pehr H. Enckell and Lars-Eric Persson actively participated and gave constant advice and criticism which contributed to the results of this work. I also want to thank Dr Torgny von Wachenfeldt, who allowed me access to the laboratory of the National Swedish Environment Protection Board, Höllviksnäs, Mrs Ylva Zachrisson who typed the manuscript, Mrs Steffi Douwes for drawing the figures and Ms Gunilla Lindquist for arrangements and help to see this manuscript published. I am grateful to late Prof. Gösta Ehrensvärd for his encouragement and financial support at the beginning of my studies.

Lastly I thank all those who contributed in some form or the other during the different phases of this work but whose names for lack of space, do not appear. I value all their help highly.

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IDOTEA IN THE SOUTHERN BALTIC; DISTRIBUTION AND
ENVIRONMENTAL FACTORS

Paper A

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Abstract

Idotea baltica, I. chelipes and I. granulosa (Isopoda) were collected at five localities at the Falsterbo peninsula in the southern Baltic. A number of environmental factors were measured at the same localities.

I. baltica and I. chelipes occurred with similar abundance, while I. granulosa was scarce. The last species was absent from the most sheltered locality, and occurred with its largest number at the most exposed locality. I. baltica dominated at the two most exposed localities. I. chelipes made up over 90 % of the numbers in the most saline locality.

Winds were dominantly westerly during summer-autumn and easterly during winter-spring. Since the localities were mainly exposed towards westerly directions, turbulence was highest during summer-autumn. Topographical differences caused the localities to be differently effected by winds; for example turbulence was lowest at the most sheltered locality.

Low water levels dominated during spring and summer. The oxygen content of the water was higher at the exposed localities, while temperature and salinity were higher at the more sheltered locality. Salinity values were unstable at all localities, however. Strong seasonal fluctuations occurred in temperature, salinity and wind.

The occurrence of the species is discussed with reference to the various environmental factors; it is concluded that exposure and salinity are the main factors determining the differential distribution

1. Introduction

Idotea species from brackish water habitats are faced with considerable variations in the environmental factors. Laboratory experiments have shown that their life processes are affected in various degrees by such variations (Naylor 1955, Jones 1974, Harvey et al. 1973, Oertzen 1973, Bulnheim 1974, Vlasblom et al. 1977). The distribution of the members of the estuarine fauna are determined by daily and seasonal fluctuations in e.g. the salinity gradient (Dahl 1948, 1956, Segerstråle 1951, 1953, Kinne 1964, 1966), and correlated to exposure (Sywula 1964, Muus 1967). The degree of exposure also influences the growth and distribution of the marine plants which are the habitats for Idotea spp. (Wachenfeldt 1975).

The life histories and distribution of the Scandinavian brackish water species of Idotea are generally well known. This is the basis of the present investigation of a group of closely related and co-existing species as regards relations to varying environmental factors in some selected habitats in southernmost Sweden.

2. Material and study areas

The euryhaline species of Idotea occurring at the localities investigated are I. baltica (Pallas), I. chelipes (Pallas) and I. granulosa (Rathke). Their distribution among the localities is given in Tab. 1. The following localities were investigated:

Table 1. Occurrence of species of Idotea in percentages at the localities investigated (1976).
Number of animals are given in brackets.

Localities Species	A Foteviken	B Fiskhamn	C Segelskären	D Kämpinge	E Stavstensudde	Σ
<u>I. baltica</u>	8.6 (52)	23.9 (290)	52.6 (884)	25.5 (229)	75.4 (1778)	...
<u>I. chelipes</u>	91.4 (554)	76.0 (922)	34.4 (579)	68.0 (611)	18.4 (434)	3100
<u>I. granulosa</u>	-	0.1 (1)	13.0 (218)	6.5 (59)	6.2 (146)	424
Σ animals	606	1213	1681	899	2358	6757

Foteviken (A)

Foteviken is a shallow and sheltered bay situated on the north-eastern side of Falsterbo Channel (Fig. 1). It is about 1.0 km long and 0.5 km wide and forms a blind end of Höllviken. The depth of the narrowest part of the entrance is about one meter during the summer. The water temperature closely follows that of the air. The bottom is soft detrital material, the first 3-5 cm of the top sediment being black. A large population of birds, and fertilizers from the surrounding farms, contribute to the growth of algae and bacteria.

Until two years ago, Foteviken was the recipient of sewage from nearby industries and villages. Because of these discharges, the oxygen content has been lower than at other localities investigated. The area is dominated by southeasterly and westerly winds.



Fig. 1. Location of the study area.

The dominant macrovegetation included green algae (Enteromorpha and Cladophora) brown algae (Fucus), red algae (Furcellaria and Ceramium), and phanerogams (Zostera and Ruppia).

Höllrevet (B)

This locality is situated on the western side of the Channel near the fairway. The sampling area is about 1.0 m deep and receives sewage from purification plants. It is visited by large number of birds.

The bottom is sandy clay. The salinity is generally lower than in Foteviken but higher than in the other investigated localities. The wind conditions and macrovegetation are the same as in Foteviken.

Segelskären (C)

Segelskären is an exposed locality on the southern part of the channel. It is a bathing site, so most of the macrovegetation is uprooted. At the collecting site the depth was about 1.2 m.

Water movement is stronger than at localities A and B. Oxygen content was generally higher than in Foteviken but salinity was

lower. Because of the depth and the water movements temperature was lower than in the above-mentioned localities. The bottom is sand with scattered rocks. The dominant macrovegetation in this locality included green algae (Cladophora, Ulva, Enteromorpha), brown algae (Chorda, Laminaria, Fucus, Ascophyllum), red algae (Furcellaria, Ceramium) and phanerogams (Zostera, Ruppia).

Kämpinge (D)

The situation in Kämpinge Bay is similar to Segelskären. The salinity and macrovegetation are the same.

The bottom is hard, consisting of stones and rocks, except for the blind end of the bay which has a sandy clay sediment. Besides, there are spots of black mud.

Stavstensudde (E)

An exposed locality, about 1-2 m deep. The hard sand bottom is spotted with rocks and very large stones. The water movement is very strong, as in the Segelskären area. The salinity is generally the same as for Kämpinge and Segelskären.

Vegetation and temperature conditions are generally the same as in the two last-mentioned localities. Large numbers of birds visit the area.

3. Methods

Animal sampling

For a description of the sampling procedure see paper B.

General

Salinity, temperature, oxygen contents, exposure (turbulence) and organic contents of the sediments were measured at all five localities. In the present paper salinity values are given for all the localities, while temperature, exposure, oxygen contents of the water and organic contents of sediments have been given for Foteviken (A) and Segelskären (C) only. The former is a sheltered and the latter an exposed locality. The hydrographic values for locality B are similar to those of A and the values for D are similar to those of C. For the two representative sites A and C diel fluctuations of salinity, top sediment temperature, oxygen and water level were measured 13-15 August, 1978.

Sampling was carried out as follows: samples were taken once a month, in times of seasonal changes every fortnight. Water samples for oxygen content and salinity measurements were collected from the free water, above the bottom sediment. Temperature readings were done in the top sediment, before noon. A sample was collected from the 3-5 cm of the top sediment for determination of organic matter. The wind and water levels were obtained from the Swedish Meteorological and Hydrological Institute (SMHI), Norrköping.

From a climatic point of view 1976 was cooler than the other years around the middle of the 1970's (Tab. 2).

Table 2. Monthly mean air temperatures in the study area 1974-1978.
ave. min., row 2 = average, row 3 = ave. max.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
74	1.1 2.6 4.2	0.7 2.6 5.0	-0.2 3.3 7.5	1.2 6.9 13.1	4.7 10.3 15.9	9.2 14.5 19.6	12.3 15.5 19.4	11.6 16.4 21.3	10.4 13.6 17.1	3.9 6.8 9.8	3.9 5.6 7.3	2.5 4.6 6.6
975	2.8 - -	-1.3 -2 4.2	-0.4 2.5 6.0	1.8 5.4 9.6	6.2 11.2 16.8	8.3 14.9 20.6	13.1 18.3 23.3	12.8 19.3 25.5	10.7 15.0 19.3	6.3 8.8 11.3	1.2 3.9 6.6	1.0 3.7 6.0
1976	-3.3 - -	-2.9 -0.4 2.1	-4.1 -0.8 2.7	1.2 5.3 9.9	5.9 10.9 15.9	10.8 15.5 20.4	12.4 18.0 23.1	10.7 16.9 22.9	8.3 12.2 16.3	6.8 8.6 10.6	1.9 4.8 7.2	-3.6 -0.5 2.1
977	-2.3 -0.3 -2	-1.5 0.3 2.3	0.8 3.3 6.5	1.8 4.6 8.1	5.3 11.2 16.7	11.6 16.0 20.7	12.5 16.2 20.3	10.0 15.4 20.5	7.1 11.9 16.6	7.8 10.1 12.8	3.5 5.6 7.8	0.7 2.5 4.3
978	-0.7 - 2.8	- 2.3 -	-0.1 4.6 5.3	0.5 11.4 9.5	4.9 15.4 17.3	9.4 15.4 20.8	11.1 15.4 19.7	12.3 16.3 21.0	8.9 11.7 14.8	6.5 9.4 12.6	5.8 7.4 9.2	-3.0 -1.2 0.9

Salinity

Salinity was measured as conductivity by a wheatstone bridge (Normameter, RW with Philips electrode 9513) with earphone. The readings were made at 20°C and later translated to corresponding salinity values with the aid of International Oceanographic tables (National Institute of Great Britain and UNESCO, 1966).

Direct measurements were made with a salinity-temperature Bridge type MC 5, Electrode Switchgear, Serial No. 0143.

Temperature

Temperature was measured with mercury thermometer calibrated to 0.2°C. The air temperatures for Höllviksnäs were received from the Channel Authorities at Höllviksnäs (near locality C) and the Weather Bureau (SMHI), in Norrköping.

Oxygen

The oxygen content was determined by the standard Winkler method. Bottles with an average volume of 130 ml were used in collecting and analysing the water samples.

Wind_and_water_level

Wind frequencies and water levels were collected from the Channel Authorities at Höllviksnäs in 1974 through 1978. The frequency of each wind direction for each month is divided by a factor of 6 (the number of observations d^{-1}) to give the number of days of occurrence per year. Calm days are also included. For Foteviken, the water levels for March and June were obtained from SMHI via Dr. Bo W. Svensson, Lund. The level of November was collected directly from the SMHI station at Klagshamn.

Turbulence

Turbulence was measured at the five sampling localities according to Muus (1968). Standard-sized gypsum balls were set singly about two meters apart and were left in place for 75 min. The weight difference was regarded as a quantitative expression of turbulence. Wind direction and velocities are from the Swedish Weather Bureau (SMHI) Norrköping.

To investigate the role of salinity and temperature on gypsum solubility, some laboratory experiments were performed. Water of 0, 5 and 10 ‰ was pumped into three circulating aquaria at 5, 12 and 20°C. Weighed balls were added and were left exposed for 75 min. These salinities and temperatures were in the ranges recorded at the sampling sites. The balls were dried at 40°C for 24 h before and after the experiment.

No distinction could be made between different kinds of water movement. Turbulence is regarded as the sum of all of them.

Sediments

The uppermost 3 cm of fresh sediment were collected in one liter plastic bags and transported to the laboratory. The loss on ignition was determined after 24 hours at 105°C and 15-20 min at 550°C.

4. Results

4.1. Distribution of Idotea species

The proportions of the three species at the five localities are given in Tab. 1. Some clear differences between the localities are evident. I. granulosa is totally absent from locality A and practically absent from locality B. At the other three localities it occurs in small numbers. Its maximum proportion of the total individuals sampled is at the exposed locality C.

I. baltica dominates at the two most exposed localities C and E, while I. chelipes makes up about three quarters of the numbers sampled at the less exposed localities B and D. I. chelipes dominates the most saline locality, A, by over 90 % over the years of sampling.

In terms of abundance, I. baltica and I. chelipes were similar, while I. granulosa was rather scarce (6 % of the total number samples).

4.2. Hydrographic characteristics

Salinity

Salinity values were unstable as a result of exposure, wind and water movements. The estuarine and coastal water is mixed at times with more saline water forced southwards in the Sound by the northerly current (Dahl 1946, 1948).

Herman (1969) estimated the time for water renewal in the control part of the Sound. These estimates were based on movements of salinity fronts, direct-current measurements and for the deeper layers a phase difference in the annual temperature cycles in the Sound and the Kattegat. The surface layer to 5 m depth was renewed in 2-3 days. At 10-15 m depth, the time increased to 6 days and at 25-30 m depth, the time was about 20 (10-40) days. The time for renewal should be longer in shallow water and in bays. For Foteviken (max. depth, c. 1.5 m), Höllrevet (max. depth, c. 2.7 - 3.0 m) and Segelskären (max. depth, c. 5 m) the time taken may be slightly above 3 days.

In general, higher salinity values occurred at locality A than at the other localities (Fig. 2A). It had its maximum (13.2 ‰) in July. Comparatively high values occurred during the autumn and winter. There is a strong seasonal variation. The minimum, in early spring, resulted from melting ice, absence of thorough water mixing and persisting low water level.

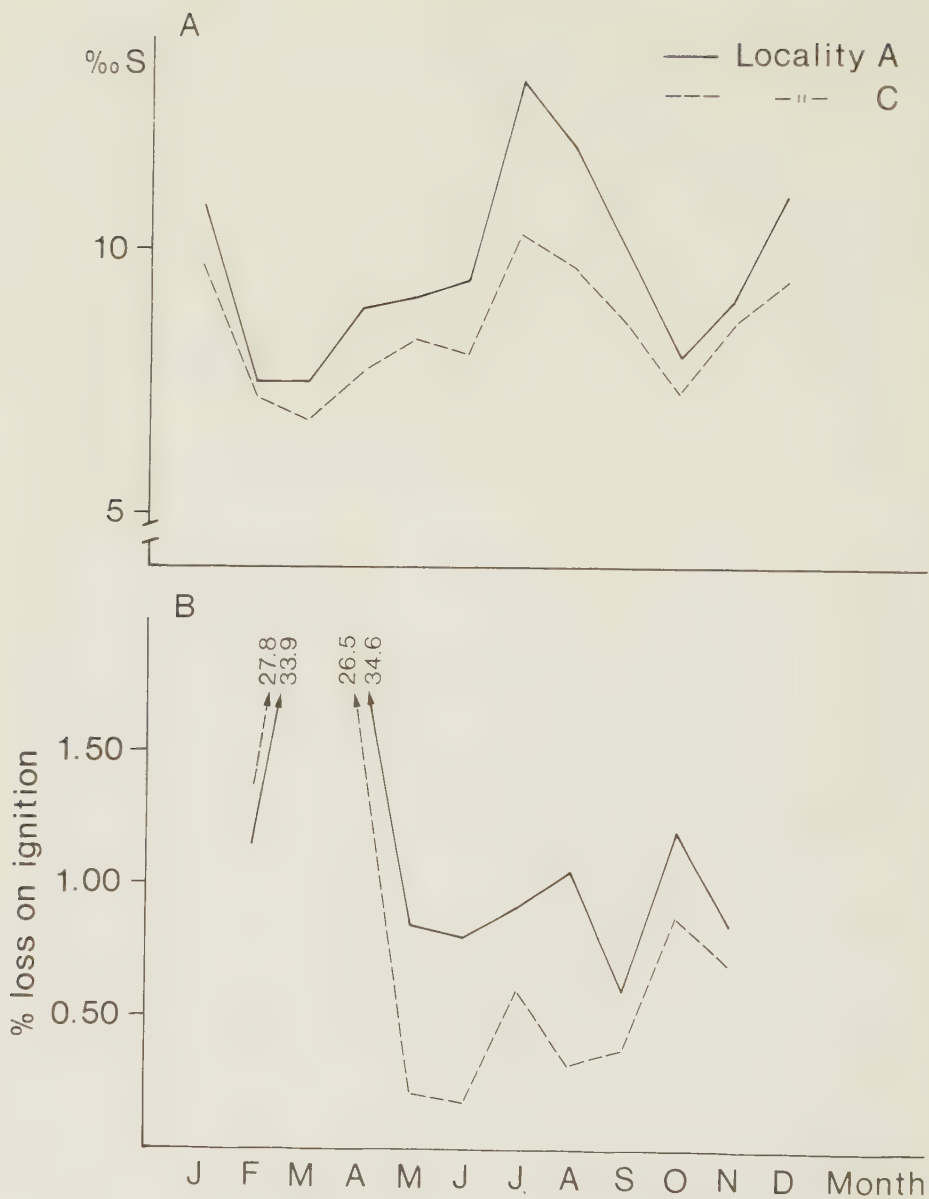


Fig. 2. Monthly salinity values (A) and percentage loss on ignition (B) in localities A and C in 1976.

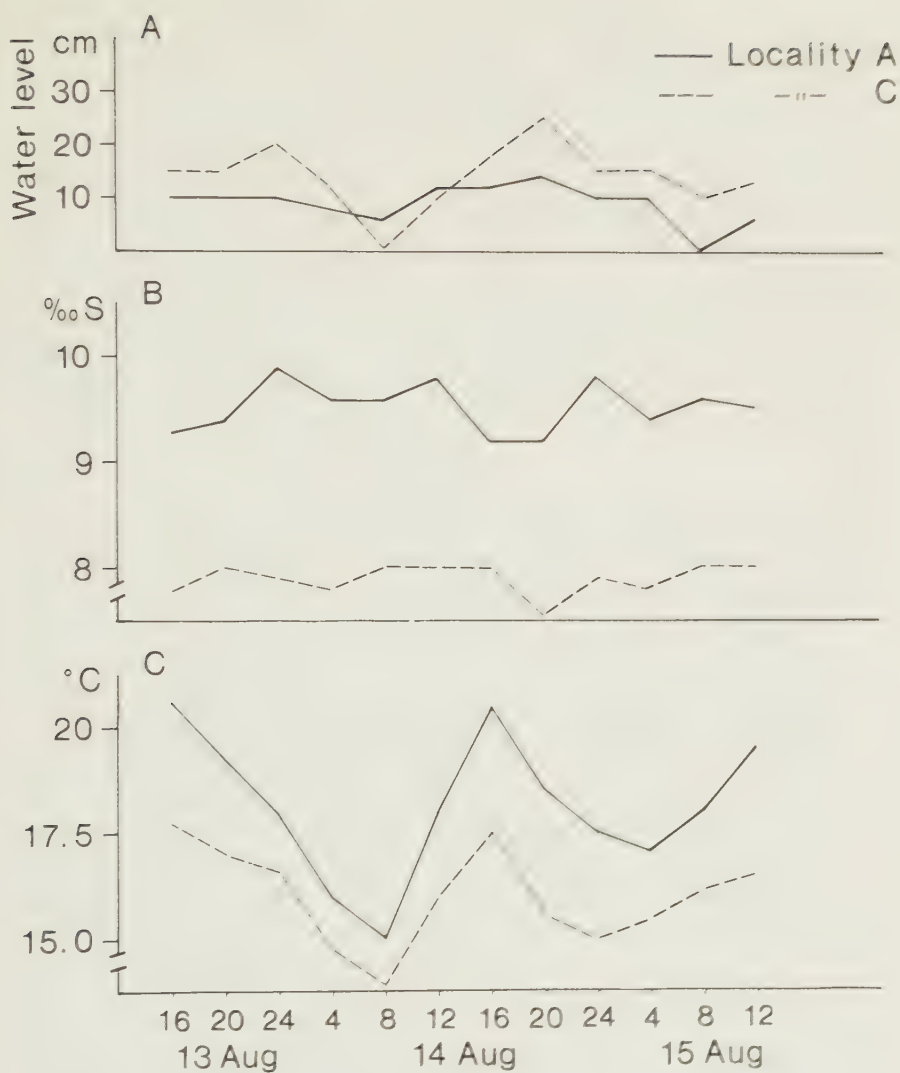


Fig. 3. Diel fluctuations in environmental factors in localities A and C from 13 August to 15 August 1978.

Fig. 3B shows the diel fluctuations in an exposed locality (C) and a sheltered locality (A). The average at locality A was $9.5^{\circ}/\text{oo}$ and at locality C below $8.0^{\circ}/\text{oo}$. The differences between the two areas were considerable, due to the exposure of locality C. The minute rise of the water level at midnight (Fig. 3A) did not result in significant increase of the salinities in any of the localities.

Temperature

Temperature varies with exposure, water depth and movements, and insolation. In the shallow localities investigated (maximum depth at Foteviken 1.5 m and at Segelskären 4.5 m) thermal stratification was absent and air and water temperatures followed each other closely. The air temperature is lower than the water temperature from January to March. With the beginning of spring, the air became rapidly warmer than the water. This continued into the summer when the maximum air temperature of 25°C was recorded in July at the same time as the maximal water temperatures were recorded in the localities. Thereafter, the water temperature and the air temperature were about the same from August throughout the autumn until in winter when the air became cooler.

The diel fluctuations were compared in two localities, one sheltered and another exposed (Fig. 3C). The daily maxima were recorded at 1600 hours with a difference between localities A and C of 9.6 %. The minima were recorded around 0400-0800 hours, with a difference of 3.5 %. Generally, the maxima as well as the minima of the water came 1-2 hours after the corresponding air temperature. The high differences between the two areas at noon illustrate the importance of water depth and shelter.

Oxygen

Generally, the oxygen content in daytime is influenced by insolation and differences in the influx of salt water. In localities A and C the values at noon vary only slightly, except in September - October when they are high. The reason might be an influx of water from Skagerak via the Sound.

A comparison between the localities shows that values recorded for July were 6.5 mg l^{-1} at locality A, 7.0 mg l^{-1} at B, 10.1 mg l^{-1} at C, 9.4 mg l^{-1} at D and 9.8 mg l^{-1} at E. The content was 55 % higher at the exposed locality C than at the sheltered locality A.

The diel oxygen fluctuations at localities A and C were compared. The variations were probably a result of photosynthesis and respiration. When measurements started at 1600 hours, the content was high at both localities. After a drop in the night an increase was recorded by 0800 hours. Early in the day, high values were noted at locality C and remained at the same level until late in the afternoon, while there was a heavy drop at the sheltered locality A in the night and an increase towards noon. The afternoon decrease was considerable in both localities and the low level remained until the observations ended at noon the next day. Temperature and salinity values were normal.

The oxygen content was higher at the exposed locality whereas temperature and salinity were higher in the sheltered area.

Wind

Fig. 4 shows the wind directions observed in the sampling areas. Southeasterly wind dominated for most of the time. For example in 1977, this wind alone accounted for 50 days, i.e. 14 % of the year and the same value in 1978. The SE wind was followed in frequency by WNW wind, with an annual percentage of 9 % in 1977 and 11 % in 1978. NE wind occurred least during the study years.

Table 3 shows the prevailing winds in the different seasons. Summer and autumn periods was dominated by westerly winds whereas winter and spring were dominated by easterly winds. Westerly winds had the highest velocities while those from the north had the lowest.

Thus, westerly winds accounted for 44 % of wind velocities between 16 and 20 ms^{-1} , 63 % of velocities between 11 and 15 ms^{-1} , and 40 % of velocities between 21 and 30 ms^{-1} .

Water level

Low water level dominated in the sampling areas during spring and summer while high water level occurred mostly during the winter months in 1975-1978. Examples for such occurrence are shown in Fig. 5A for locality B and in Fig. 5B localities A and C are compared for March, June and November. The low water level occurred from February through August with a slight increase in September. The high level continued throughout the winter.

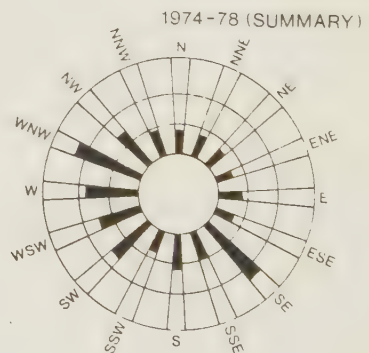
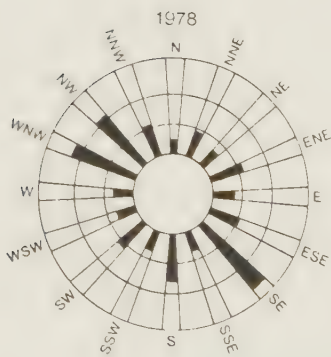
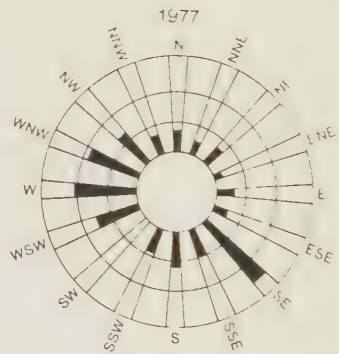
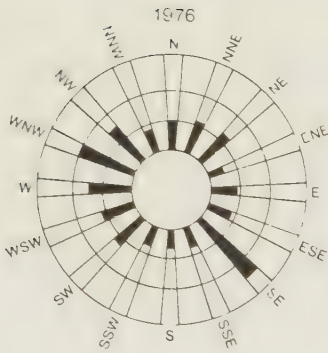
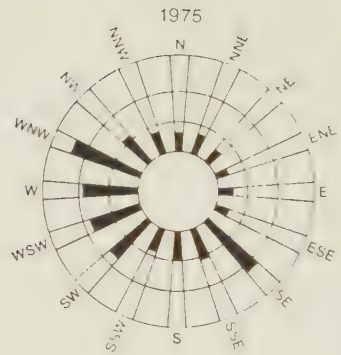
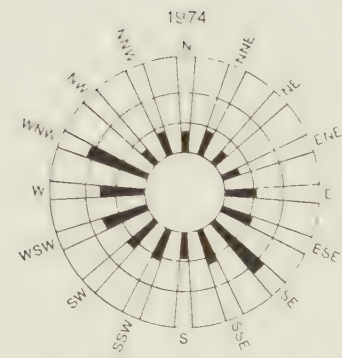


Fig. 4. Percent days with winds of different directions. Data from 1974-1978. Each concentric circle represents 5 %.

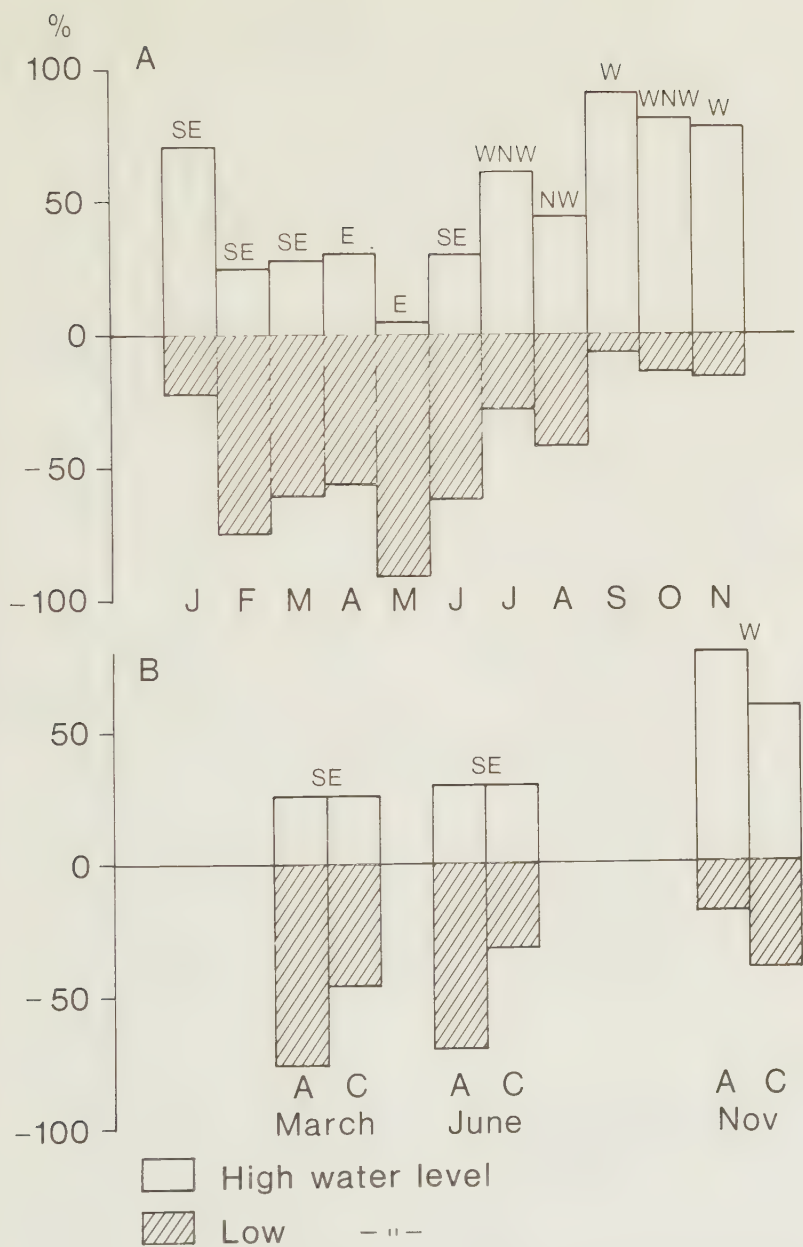


Fig. 5. Percent days with water levels above and below mean water level in loc. B (A) and locs A and C (B) in 1978. The different wind directions dominating in each month are indicated above.

Table 3. Prevailing winds under each season from 1974 to 1978.

		1974	1975	1976	1977	1978
Winter	Dec	WSW	SW	N	SE	E
	Jan	SE	SSE	W	SE	SE
	Feb	SSE	WNW	SE	SE	SE
Spring	Mar	E	NE	NE	SE	SE
	Apr	E	WNW	SE	E	E
	May	E	SE	SE	E	E
Summer	Jun	WNW	SE	WNW	SE	SE
	Jul	WNW	NW	SE	WNW	WNW
	Aug	WNW	SE	WNW	NW	NW
Autumn	Sep	SE	SW	E	W	W
	Oct	NNE	W	SE	WNW	WNW
	Nov	SW	SE	SW	W	W

Low water levels occurred in both localities A and C in March and June and they were lower in A than in C (Fig. 5B). The opposite occurred in November where high water level was observed in both areas. March and June were dominated by SE wind and November by W wind. Diel variations were higher in C than in A (Fig. 3A). The level was above the mean in both areas. Thus, the low water level at locality A in March and June is explained by the wind forcing the water out of the shallow bay.

Turbulence

The laboratory experiments showed that gypsum solubility was influenced by salinity and temperature (Fig. 6). The solubility increased more at a salinity increase from 0 to 5 ‰, than at an increase from 5 to 10 ‰. At different temperatures, the increase in solubility was higher at an increase from 12 to 20°C, than at an increase from 5 to 12°C. Thus, temperature seems to exert a stronger influence on solubility than salinity in the range experienced in the field.

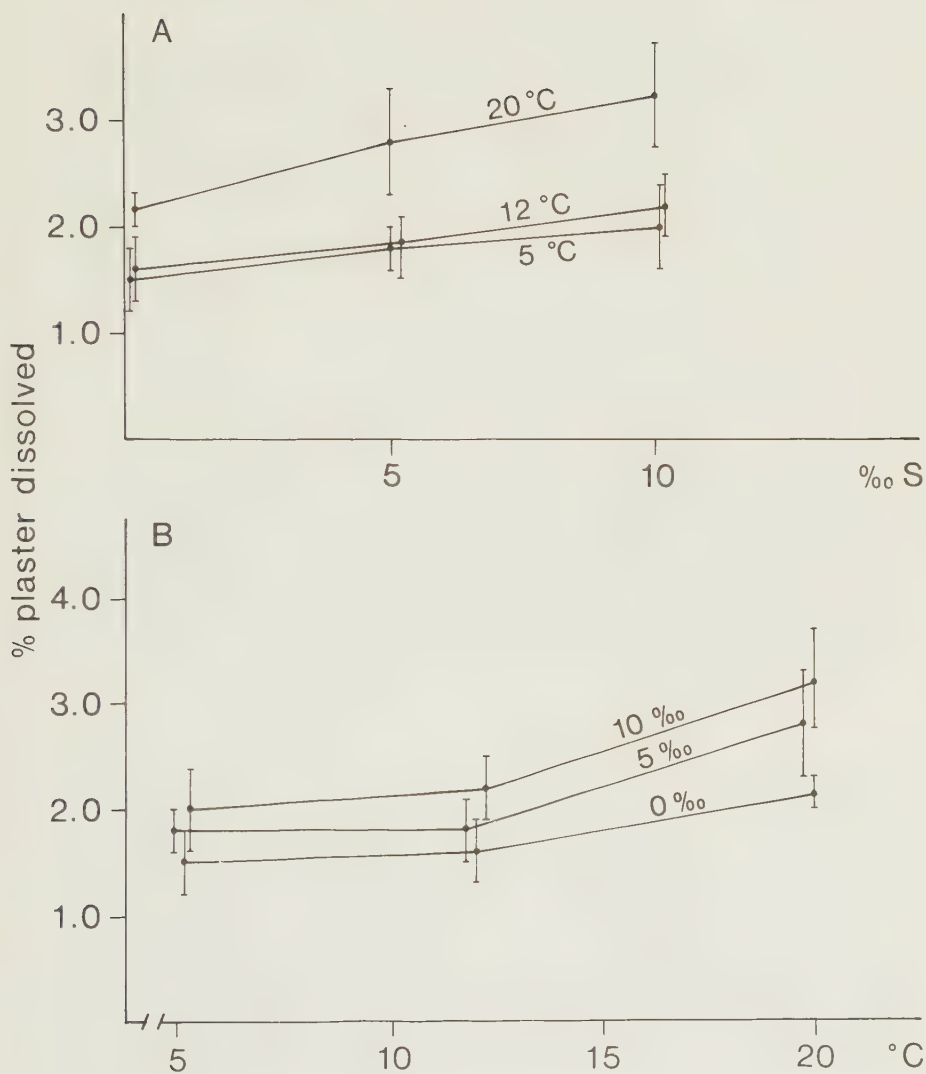


Fig. 6. Percent gypsum dissolved ($\pm$ S.D.) at different temperatures (A) and at different salinities (B).

An analysis of variance showed that salinity (irrespective of temperature), temperature (irrespective of salinity) and the salinity and temperature interaction all significantly contributed to solubility. The percentage or variation accounted for by salinity and temperature was 38.4 (12.6 % for salinity, 18.8 % for temperature, and 7.0 % for interacting salinity and temperature). Thus, the residual solubility, i.e. solubility accounted for by other factors (mainly water movement), was 61.6 %.

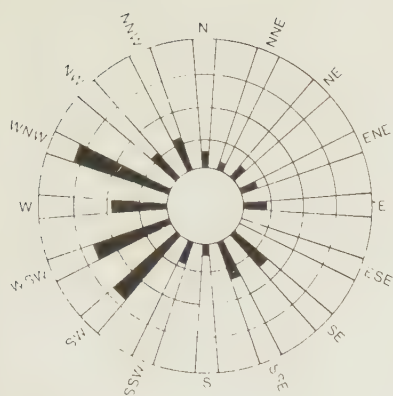
In the field it was evident that the gypsum solubility was indirectly influenced by the wind directions (Fig. 7). Solubility was higher with westerly winds and lower with easterly winds. Winds between SW-W-NW accounted for 53% of the total amount dissolved. Taking into account that these directions also account for a large part of the high velocity winds, it is clear that water movement is reflected in the amounts of gypsum dissolved.

The localities have different topography and are differently exposed, and it is clear that each locality was dominated by a particular wind direction, which meant a maximum amount of gypsum dissolved. For example, the largest amount dissolved at locality A coincided with WNW winds. These winds also forced the water into the shallow bay, and thus caused turbulence. On the other hand, the generally sheltered character of locality A caused the total amount of gypsum dissolved to be lower than at the other localities.

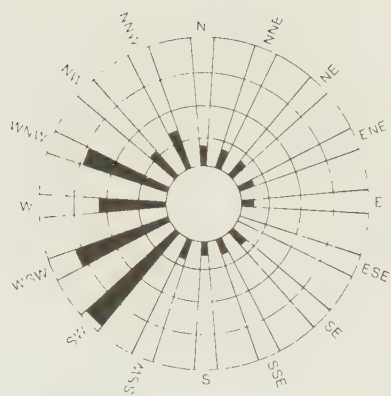
Sediment

The amount of organic matter in the sediment is given as percent loss on ignition. Fig. 2B shows the monthly percentages in localities A and C. The sediment in the sheltered locality (A) had higher organic content than that observed in the exposed locality (C). The values in March and April were extremely high. There was a drop between April and May in both areas. An increase was observed in July which continued to August, and it dropped again in September and November. Organic content in locality C decreased in August but later increased from September to October only to drop again in November.

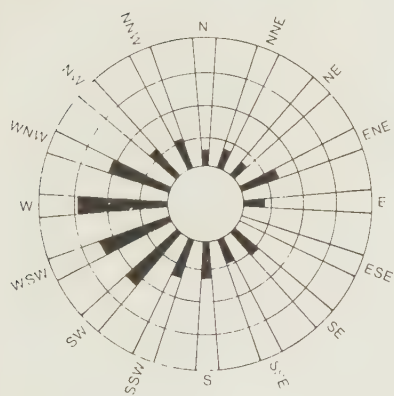
Table 4 gives sediment characteristics observed in the upper 3-5 cm from locality A. The percentage loss on ignition started to increase about 50 m from the shore, which may indicate an increased sedimentation of organic matter outside the zone of turbulence.



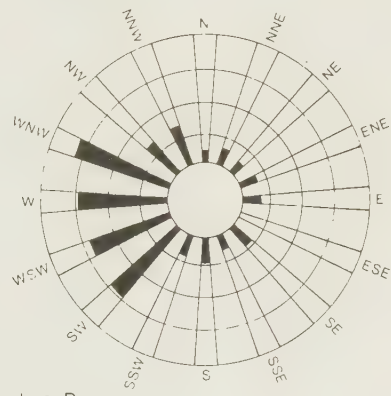
Loc. A



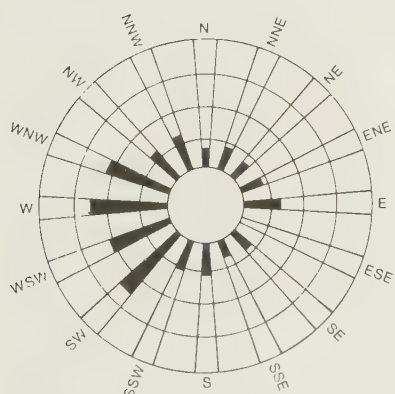
Loc. B



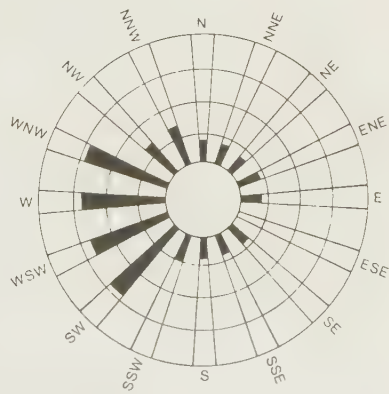
Loc. C



Loc. D



Loc. E



SUMMARY

Fig. 7. Percentages of gypsum dissolved at different wind directions at the five study localities. Each concentric circle represents five percent. Measurements made in 1978.

Table 4. Loss on ignition in locality A.

Sediment characteristics (sediment cores, upper 5 cm):										
Sample No.	1	2	3	4	5	6	7	8	9	10
Distance from shore (m)	0	10	20	30	40	50	60	70	80	90
Temp. (°C)	19.5	19.4	19.3	18.5	18.5	18.5	18.5	18.7	18.4	18.4
Depth (cm)	17	24	27	31	35	39	45	45	53	63
Salinity (‰)	9.2	9.3	9.4	9.3	9.6	9.4	9.4	9.4	9.6	9.6
Water content (wt %)	21.60	21.08	20.54	21.75	20.00	17.44	19.93	21.63	17.97	23.40
Loss on ignition (%)	1.23	1.30	-	1.20	1.13	0.95	0.98	1.29	1.37	2.67

4.3. Factors affecting the distribution of Idotea spp.

Salinity

Many estuarine animals are restricted in their distribution by a number of environmental factors among which salinity is the 'ecological master factor' (Kinne 1966). Abundance of species decreases along salinity gradient (Segerstråle 1951, 1953, Dahl 1948, 1956).

The Idotea species in the Baltic are distributed from areas of varying salinities. Sywula (1964) collected I. chelipes in a salinity of 6.5 ‰ while I. granulosa was found in small numbers. He observed that I. chelipes was expelled to localities where salinity could drop to almost zero and was therefore restricted in its distribution by more vital species, I. baltica and I. granulosa, which demanded higher salinities. He further distinguished between the minimum absolute salinity tolerated and the minimum mean salinity required to maintain life. For I. chelipes, the minimum absolute salinity tolerated was 0.2 ‰ whereas I. baltica and I. granulosa tolerated 4.0 ‰. The minimum mean salinity was 3.6 - 6.2 ‰ for I. chelipes and 4.3 - 7.3 ‰ for both I. baltica and I. granulosa. The marine species were restricted in their distribution by lower salinities. The lowest salinity noted by Muus (1967) for I. chelipes was 4.5 ‰. He got specimens of I. baltica in Kysing Fjord with salinity of 22-24 ‰ and in Dybsø Fjord of 10.0 ‰. In the Gulf of Bothnia and in the Finnish Bay, I. baltica was more restricted by 3-4 ‰ S-isohaline than I. chelipes (Segerstråle 1944). He also found the three species in the Baltic in salinities as low as 6.5 ‰ for I. granulosa and 3.5 ‰ for I. baltica and I. chelipes.

From my collections in the southern Baltic, I. chelipes and I. baltica were found in locality A, where salinity dropped to about 4.5 ‰ in 1976 when the ice had melted. I. granulosa, however, was always collected in higher salinities, between 6.0 - 6.8 ‰. From the northern Baltic, I. baltica and I. chelipes were collected in 1-2 ‰ and I. granulosa in 4.0 ‰ before the breeding period (Salemaa 1979).

Bulnheim (1974) collected I. baltica from the Lübeck Bay (Baltic Sea) with a salinity of 15.0 ‰. Idotea baltica was limited in its distribution in Finland by the isohalines of 3-4 ‰ and in Randers Fjord by 10-15 ‰ (Johansen 1918, Spärck et al. 1933, see Muus 1967, p. 227). I. chelipes were collected on the Isle of Man where salinity fluctuated between 6.8 and 29.5 ‰ (Naylor and Slinn 1958). All these observations indicate the euryhalinity of the Baltic species of Idotea.

Laboratory experiments show that the Idotea species can tolerate a wide range of salinities. Naylor (1955) showed that they could tolerate salinities above 35.0 ‰. I. chelipes endured salinity twice that of the sea water but could not sustain salinities below 4-6 ‰. In the range of 18-53 ‰ at 10-14°C, over 80 % I. granulosa survived more than 48 h whereas a lesser percentage survived in 53-61.2 ‰ and 8.7-18 ‰. Less than 80 % of I. chelipes survived between 4.5 - 8.7 ‰ and 43.7 - 52.5 ‰, over 80 % survived in 8.7 - 43.7 ‰ after 48 h but only a few survived salinities between 52.5-70 ‰.

Oertzen (1973) found that I. baltica could tolerate 6-34 ‰ at 5°C and I. chelipes could tolerate 5-42 ‰ at 5°C with high survival. Vlasblom et al. (1977) found that survival of I. chelipes decreased very strongly below 14.0 ‰. Kronstedt (unpubl.) also found that I. chelipes survived only a short time in 1.8 ‰ but longer in salinities above 9.8 ‰. All the animals died within six hours in distilled water. In my experiments with salinity tolerance at different temperatures, 47 % of I. chelipes survived in 3 ‰ at 20°C after 7 h while I. baltica and I. granulosa had 100 % mortality within the first hour. In another experiment in 0.3 ‰ at 20°C, 43 % I. baltica, 27 % I. granulosa and 100 % I. chelipes survived after the first hour. In general, my experiments showed that all three species tolerate intermediate salinities and temperatures best, and higher salinities (up to 22.5 ‰) better than low salinities (0.3 and 3 ‰). Jones (1974) found that I. chelipes survived well in reduced

salinities with 80 % survival at 25 ‰ s.w. whereas I. granulosa was less tolerant with an equal survival rate down to 50 ‰ s.w. I. chelipes could survive for several hours in distilled water and had 60 % survival in 10 ‰ s.w. after 9 days. In 100 ‰ f.w. Packington (1934, unpubl.) showed that all I. granulosa died within 3 h and in 90 ‰ f.w., all were alive but inactive three days later. The optimal range was apparently 60-70 ‰ f.w. The general conclusions that can be drawn from literature data and my own (unpubl.) experiments are, (1) that I. chelipes has a more efficient osmoregulation than I. baltica (and probably also than I. granulosa) and (2) that I. granulosa is probably a weaker competitor than the other two species. The latter statement is also supported by the data in paper C.

Temperature

In combination with salinity, increased water temperature reduces osmotic resistance to brackish water (Schlieper 1958, see Muus 1967). Bulnheim (1974), testing the response of I. baltica to temperature stress found that when a sudden transfer was made from 15° C to 5° C, the new metabolic steady state was reached within c. 3 h but when transferred from 5° C to 15° C, the same steady state was reached in 15 h. At this temperature, there was a slight decrease in respiration rates.

Forsman (1956) stated that the local distribution of the Idotea species was influenced by temperature. In my collections from the southern Baltic, the abundance near the shore was greatly influenced by temperature. Several hours of search in the Fucus during winter could yield a catch of only 1-2 specimens. Similar observations were made by Howes (1939) in England. To escape the harsh winter temperatures, Idotea species migrate to deeper water with higher temperatures.

Due to the shallowness in locality A, large thermal fluctuations in combination with a periodically low salinity probably explains the absence of I. granulosa from that area.

Turbulence

The distribution of the Idotea species is influenced by exposure (Segerstråle 1944, Naylor 1955, Sywula 1964, Muus 1967). As noted by Muus, the distribution of I. baltica was governed, directly or indirectly, by water movements (see also Muus 1967 p. 116) while

I. granulosa 'preferred' lotic habitats with I. chelipes in lentic biotops. Sywula (1964) gave I. baltica as preferring medium to strong exposure while I. chelipes was resistant to wave action. Forsman (1956) mentioned I. granulosa being very numerous in areas of strong water movements. This supports my findings, that I. granulosa was present only at the exposed localities C-E. According to Muus (1967) I. chelipes is found from strong currents to stagnant water. It is not surprising why I. chelipes was dominant in locality A which is weakly polluted. In this station, I. granulosa was not represented and I. baltica was found in smaller numbers.

Oxygen, sediment, water level

Except in stagnant waters where there is no water movement, the surface layers is often saturated with oxygen and deficiency is rather improbable (Kinne 1970). Oxygen is therefore not a limiting factor in the surface waters of the Baltic where there is good water circulation, e.g. in the sampling areas.

Water level changes influence renewal of water. This is often connected with changes in salinity. In the areas investigated low water level often occurs during the spring and summer and high water level during the winter. The salinity amplitude is within the range of tolerance for the Idotea species, except for I. granulosa at locality A.

The type of sediment in an area indicates the strength of the water movement. Soft bottom is found in locality A. Since Idotea species are not sediment dwelling species, the effect of sediment therefore is of secondary importance.

5. Concluding remarks

The environmental factors dealt with are interrelated and complex. The influence of one factor cannot be isolated from the rest as all these factors interact, increasing or decreasing the effect of each other. For example, variations in temperature contribute to variations in air pressure which in turn influences the water level. Likewise, variations in temperature cause wind which in turn influences the water movement and this factor again influences the salinity.

Salinity and temperature

Since the Baltic is tideless, most of the fluctuations in salinity are caused by local winds and water movements. Source of such salinity fluctuations in the Baltic is caused by the inflow of more saline water from the North Sea and the outflow from the Baltic reaching a salinity level of 8 ‰ as it approaches the Sound (Dahl 1948). The high values recorded from the sheltered locality are most probably caused by evaporation, and strengthened by sewage and discharges from industry and run-offs from the vicinity. The inorganic contents settle at the bottom in the soft sediment and as water movement becomes stronger, the inorganic salts get into solution, thereby increasing the salinity concentration. Higher values recorded in autumn and winter are probably influenced by the influx of the saline water from the North Sea. However, the drop in salinity observed at the end of winter and the beginning of spring can be caused by dilution as a result of melting ice or from run-offs.

The large temperature amplitude at locality A can probably be explained by the shallowness of the locality. As a result the water temperature becomes closely related to the air temperature.

Oxygen

Oxygen content fluctuations can be influenced by several factors, e.g. the method of collection and analysis, water movement, presence of chemical pollutants and temperature.

Pollutants from agriculture and industry into locality A could have contributed to the low values recorded in that area.

The dissolved oxygen content is a function of temperature, pressure, salinity and biological activities (Zobell 1946). Since metabolism is correlated to temperature, an increase in temperature, therefore, results in a higher oxygen consumption leading to lower values during the summer. But the summer values can be equally influenced by escape of oxygen from water into the air. If the air temperature is lower than the water, e.g. in summer, then more oxygen escapes from the water into the atmosphere. The reverse occurs during the winter, leading to higher values.

The presence of vegetation can greatly influence the oxygen fluctuation and this could be one of the main factors contributing to the differences in the oxygen content between localities A and C. Oxygen is reciprocally correlated to the carbon dioxide

content. Fluctuations in one system affects the other. And these two systems greatly influence the distribution of many brackish species.

With good water movement, oxygen is not a limiting factor and deficiency in oxygen leading to mortality has not been reported from the surface waters of the Baltic (Kinne 1970).

Wind, water level and turbulence

Lisitzen (1963) computed the increase in the water level of the Baltic compared to the mean sea level to be 7.9 cm due to the specific density. Increase in air temperature is usually accompanied by a decrease in atmospheric pressure and greater precipitation, thus increasing the sea level while a decrease causes an increase in atmospheric pressure and lower precipitation leading to lower sea level (Miller 1958).

The westerly wind moves the less saline surface water towards the shore while a strong easterly wind may bring even the bottom current to a halt. During long periods of W wind the amount of water in the Baltic increases while the E wind lowers its level. Turbulence and water movement is thus differently influenced by different wind directions. Thus, as could be expected, water movement was stronger in the exposed locality than in the sheltered locality.

Sediment

The high organic content recorded from the sheltered locality can be the result of weak water movement as most of the suspended matter is deposited whereas in the exposed locality C, with stronger water movement, the organic matter is not deposited at all. Differences in the water movement led to differences in the organic content in the sediment.

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LIFE HISTORY AND FECUNDITY DIFFERENCES IN IDOTEA BALTICA,

I. GRANULOSA AND I. CHELIPES IN THE SOUTHERN BALTIC

Paper B

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Abstract

The population dynamics of Idotea baltica, I. granulosa and I. chelipes in the southern Baltic was examined from 1975 through 1977. The duration of the breeding season in I. granulosa was shorter than in I. baltica and I. chelipes. I. granulosa produced only one cohort while the other species each produced two. Fecundity was correlated to female size. Thus, I. baltica had maximum 138 eggs, I. granulosa 116, and I. chelipes 95. However, if females of equal size were compared there was 40 eggs/? in I. baltica, 45 eggs/? in I. granulosa and 54 eggs/? in I. chelipes in the size class 3-4 mm. Fecundity decreased for all species during the breeding season. Sex ratio ($\delta/\text{?}$) was generally at a minimum during the summer month.

A difference between number of eggs and number of embryos in the marsupia of I. baltica and I. chelipes was recorded. It is suggested that fungi infecting the eggs are partly responsible for this loss of eggs during the incubation period.

1. Introduction

Three Idotea species occur in the southern Baltic on Fucus and Cladophora vegetations; the marine forms I. baltica (Pallas) and I. granulosa (Rathke) and the brackish water species I. chelipes (Sywula 1964b). I. granulosa is restricted to exposed localities, while I. chelipes can survive in lentic areas of fluctuating salinities (Muus 1967).

Some aspects of their biology studied in the Baltic include taxonomy (Sywula 1964a), ecology and zoogeography (Sywula 1964b, Muus 1967, Jansson 1969, Jansson and Matthiesen 1971), breeding and bionomics (Jancke 1926, Jazdzewski 1970, Betz 1974, Haage 1975, 1976, Salemaa 1979). There is further information on the ecology and bionomics of the species in Britain (Howes 1939, Naylor 1955c, Naylor et al. 1961), France (Labourg 1971) and North America (Strong 1978).

The present study examines the seasonal fluctuations in abundance and fecundity of the three Idotea species in southern Baltic.

2. Material and method

2.1. Study area

Five localities around the Falsterbo peninsula in the southern Baltic were studied. (Fig. 1). These were Foteviken (A), a shall-

ow and sheltered bay with large amounts of organic material on the bottom. Due to high temperatures and low water turnover, the oxygen content can be low during the summer months.



Fig. 1. Map showing the sampling localities.

Höllrevet (B) is also a rather shallow locality (c. 1 m deep), which receives sewage from purification plants. Bottom substrate is sandy clay. Segelskären (C) is a more exposed locality. It is used for recreation bathing, so much of the vegetation is uprooted. At the collection site the depth was c. 1.2 m. Bottom substrate is sand and oxygen content is high throughout the year. Kämpinge bay (D) is rather similar to Segelskären except that there are more stones and rocks on the bottom in Kämpinge. Stavstensudde (E) is also an exposed locality, about 1-2 m deep, with a hard sand bottom with occasional rocks and very large stones. The water movement is very strong as in Segelskären.

Salinity was generally highest (6-12 ‰) in localities A and B. Localities C - E had a salinity of 5-8 ‰. For a more detailed description of localities see Korheina (paper A).

For a general description of the temperature and salinity fluctuations in locs A and C, see Fig. 2.

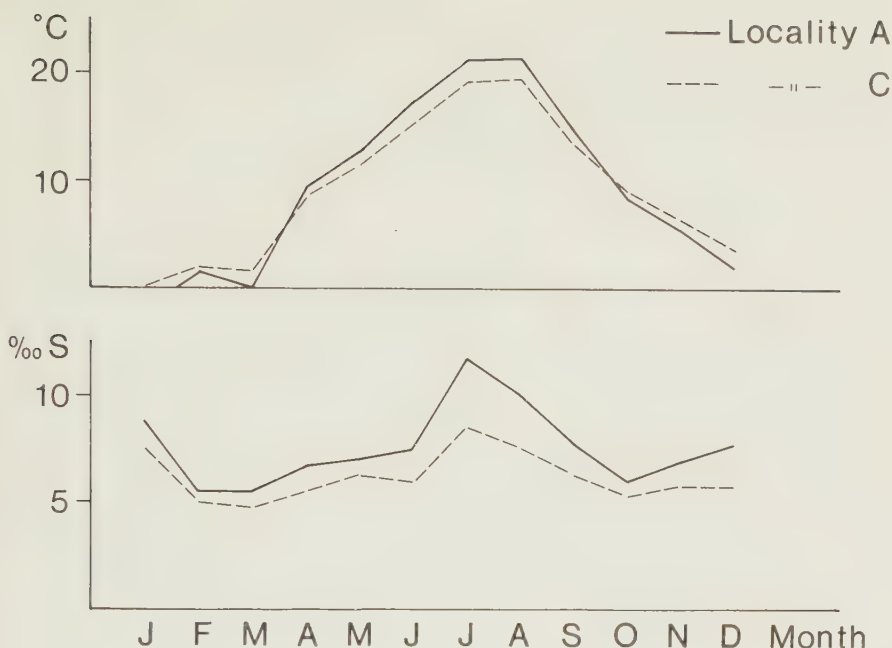


Fig. 2. Temperature (above) and salinity fluctuations (below) for different months in locality A and C.

2.2. Sampling, measurement and preservation

Samples were collected monthly with a hand net (meshsize 0.25 mm) from 1975 through 1977. The animals were sampled from attached algae (*Fucus vesiculosus*, *F. spiralis*, *F. serratus* and *Cladophora rupestris*) and from *Ruppia spiralis* and floating *Fucus* species. The algae were shaken successively into the net and the animals collected in plastic containers. During the summer the whole algal bush was transported in plastic bags to the laboratory where they were thoroughly washed under running water, the animals sorted out and preserved in 5 % formalin. A similar method of preservation was used by Strömberg (1965) and Naylor (1972).

At the end of autumn and especially in December, animals became so scarce that sampling became difficult. Several hours of search could result in collecting only 1-2 specimens from under stones. In areas without stones not a single specimen could be found.

For examination, animals were washed and individually measured under a dissecting microscope, in extended form from the anterior of cephalon to the tip of telson to the nearest 0.1 mm. Similar methods have been used for other isopods (Steel 1961, Strong 1978). Ovigerous females were both weighed and measured in 1977.

2.3. Identification

The animals were identified according to Sywula (1964a) and Naylor (1972). The material was classified to species, sex and size categories. The males were identified by the presence of appendix masculina on the second pair of the pleopods. Some males of I. baltica had some black spots on the penes muscularis not observed in the other two species. The males of the three species were larger and less pigmented than the corresponding females.

Juveniles or indeterminates apply to post-marsupial stages in which identification by sexual characteristics was not possible. All animals, not being juveniles but without appendix masculina were classed as females. These females were grouped as either immature or mature. The former were below the minimum size for breeding and the latter were divided into the following groups:

1. Females with eggs or embryos. The term "egg" is used in this study synonymously with "embryo" representing all marsupial developmental stages. The eggs or embryos were extracted with a pipett, counted, and the females measured and weighed.
2. Females without marsupia.

3. Results

3.1. Life cycle

3.1.1. I. baltica

Idotea baltica had two cohorts in the southern Baltic (Fig. 3, Tab. 1). Females started developing marsupium in March, and the first females with eggs appeared in May. Incubation time of eggs seemed to be between 15 and 30 d as still no juveniles were found 15 d after the first ovigerous females had appeared. However, after 30 d (29 June) there were 18.6 % juveniles in the population indicating hatching from eggs of the first cohort. This hatching continued through the next sampling (13 July) after which there was a sharp decrease in number of juveniles. The second cohort appeared at the end of August but this cohort seemed to be smaller than the first. Reproduction continued, although at a much lower

Table 1. Fecundity of the *Idotea* species in 1977.

		Σ ♀ with embryos	Σ ♀ with eggs	Σ ♀ with fungi	Σ ♀ with ovigerous	Σ ♀ with empty marsupia	Σ ♀ non-ovigerous	♀ ovigerous / ♀ non-ovigerous	Σ juveniles 2-5 mm	Σ ♀ immature 5-8 mm	Σ ♀	Σ ♂	♀ Sex ratio
<i>I. baltica</i>	Feb	-	-	-	-	-	89.9	-	-	11.1	48.7	51.4	1.1
	Mar	-	-	-	-	-	93.5	-	-	6.5	45.5	54.5	1.2
	Apr	-	-	-	-	-	92.9	-	-	7.1	40.3	59.7	1.4
	May	3.6	8.8	5.7	18.1	0.6	81.3	0.2	-	5.7	36.2	63.8	1.8
	Jun	39.2	17.3	17.9	74.5	18.5	7.0	2.9	18.7	0.3	66.4	33.6	0.5
	Jul	28.1	14.0	31.6	73.7	15.8	10.5	1.6	41.0	46.2	85.5	14.5	0.2
	Aug	24.2	15.2	12.1	51.5	27.3	21.2	1.1	11.6	58.8	70.2	29.8	0.4
	Sep	18.8	18.8	7.9	39.5	42.1	18.4	0.7	24.1	47.1	75.9	24.1	0.3
	Oct	13.5	-	-	13.5	1.4	85.1	0.2	1.4	21.3	44.6	55.5	1.2
	Nov	6.3	-	-	6.3	6.3	87.5	0.1	-	3.0	40.7	59.3	1.5
<i>I. chelipes</i>	Feb	-	-	-	-	-	100.0	-	-	-	35.9	64.1	1.8
	Mar	-	-	-	-	-	100.0	-	-	-	48.1	51.9	1.1
	Apr	-	-	-	-	-	100.0	-	-	-	72.7	27.3	0.4
	May	22.5	30.0	-	52.5	2.5	45.0	1.1	-	-	60.6	39.4	0.7
	Jun	38.9	19.4	16.7	75.0	16.6	8.5	3.0	31.2	17.4	58.0	42.0	0.7
	Jul	32.3	28.0	0.9	61.2	2.5	43.4	1.6	19.1	4.9	64.6	35.4	0.6
	Aug	51.9	17.5	13.7	83.1	13.7	3.3	4.9	7.5	2.6	69.5	30.5	0.4
	Sep	9.0	9.0	32.8	50.8	28.4	20.9	1.0	24.6	74.5	46.8	53.2	1.1
	Oct	33.2	4.4	-	37.5	4.4	58.2	0.6	1.1	19.8	33.0	67.1	2.0
	Nov	10.2	-	-	10.2	18.8	71.1	0.1	-	-	45.7	54.3	1.2
<i>I. granulosa</i>	Feb	-	-	-	-	-	100.0	-	-	-	54.6	45.5	0.8
	Mar	-	-	-	-	-	100.0	-	-	-	42.0	58.0	1.4
	Apr	-	8.6	2.9	11.4	-	88.6	0.1	-	-	72.9	27.1	0.4
	May	37.5	25.0	-	62.5	-	37.5	1.7	-	-	61.5	38.5	0.6
	Jun	7.7	38.5	15.4	61.5	7.7	30.8	1.6	61.0	29.7	67.3	32.7	0.5
	Jul	5.9	-	-	5.9	58.8	35.3	0.1	63.1	15.0	64.5	35.5	0.6
	Aug	-	-	-	-	-	10.3	-	24.6	89.7	60.4	39.6	0.7
	Sep	-	-	-	-	-	30.0	-	-	70.0	47.6	52.4	1.1
	Oct	-	-	-	-	-	69.2	-	-	30.8	43.3	56.7	1.1
	Nov	-	-	-	-	-	100.0	-	-	-	33.3	66.7	2.0

intensity, even in November. After the first cohort, many adult females died and thus presumably only produced one brood.

Growth rate of juveniles during the summer months were c. 2.5 mm per month for males and 2.1 mm per month for females. Thus the first cohort reached adult size (c. 10-12 mm) in September when some eventually could produce a second generation. Total length of the breeding season was 20-23 weeks in 1976 (Fig. 6).

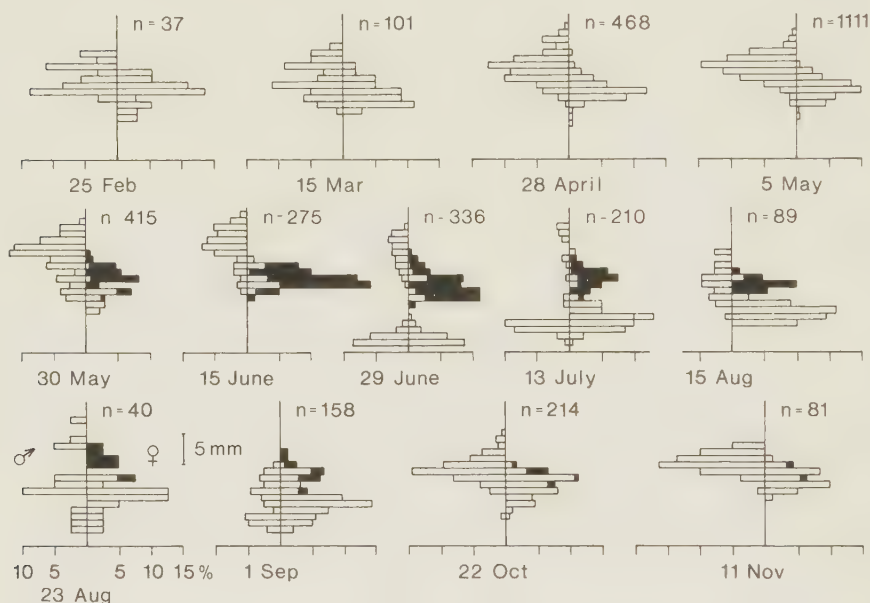


Fig. 3. Frequency of male and female *Idotea baltica* during 1977. Black bars indicate females with eggs. Animals from all localities are pooled. When sex determinations was not possible bars are centered.

3.1.2. *I. chelipes*

The life cycle of *I. chelipes* was similar to *I. baltica* except that the breeding season was somewhat longer. In 1976, the length of the breeding season was 23-25 weeks for *I. chelipes* (cf. *I. baltica* 20-23 weeks and *I. granulosa* 14-15 weeks) (Fig. 6). In May over 50 % of the females were carrying eggs which were released as juveniles in June. Of the total animals collected, 31.2 % were juveniles in June, 19.1 % in July, 7.5 % in August and

24.6 % in September. Thus, it seems as if also I. chelipes produced two cohorts; one in early summer (June) and one in late summer (September) (Fig. 4).

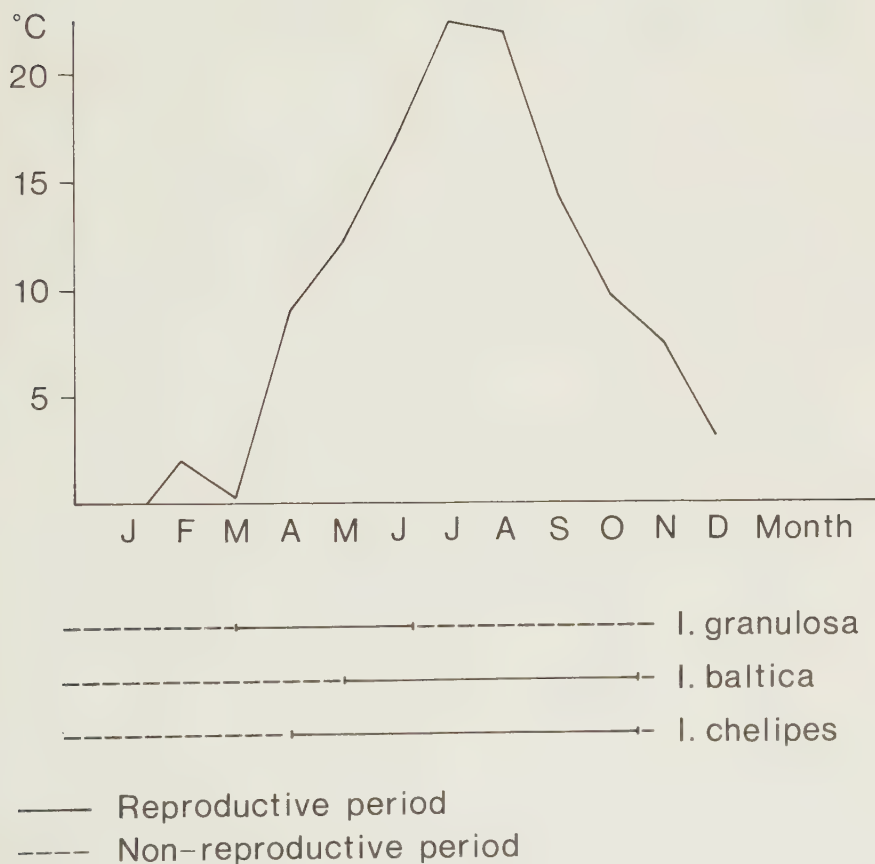


Fig. 6. Duration of the reproductive period in Idotea baltica, I. chelipes and I. granulosa in relation to water temperature. Material from locality E.

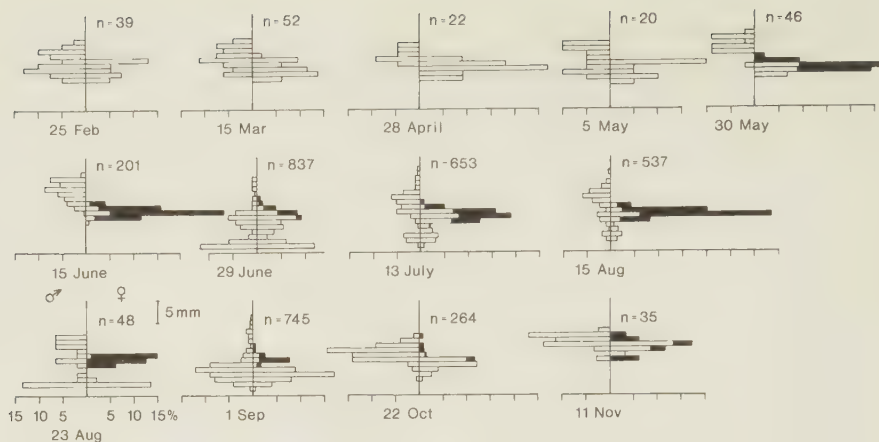


Fig. 4. Frequency of male and female Idotea chelipes during 1977. Black bars indicate females with eggs. Animals from all localities are pooled. When sex determination was not possible bars are centered.

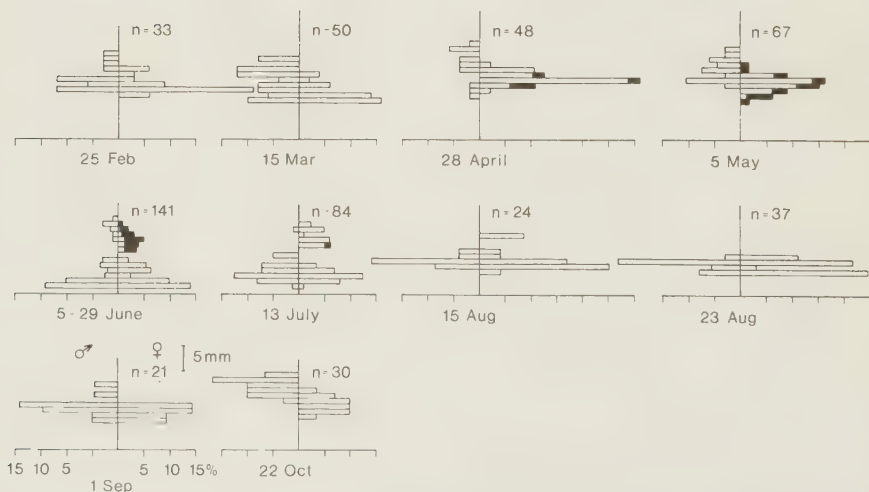


Fig. 5. Frequency of male and female Idotea granulosa during 1977. Black bars indicate females with eggs. Animals from all localities are pooled. When sex determination was not possible bars are centered.

3.1.3. I. granulosa

The life cycle of I. granulosa differed from the other two already described. Its breeding period was much shorter, but started earlier (April through July). Samples from locality E on the 28 April 1977 showed ovigerous females. In May, 37.5 % of all mature females had embryos and an additional 25.0 % had eggs (Tab. 1).

I. granulosa had only one cohort hatching at the turn of June/July. Of the animals collected, 61.0 % and 63.0 % consisted of juveniles in June and July, respectively. The c. 2.0 mm juveniles released in June were 3.0 - 4.0 mm by July. The old generation died after reproduction since only juveniles and immatures were collected after August (Fig. 5). By October and November the juveniles released in June had grown to 10-15 mm (males) (1.67 - 2.5 mm per month) and 6.0 - 12.0 mm (females) (1.0 - 2.0 mm per month).

3.2. Fecundity

The appearance of ovigerous females differed between localities and species. I. granulosa were always the first to appear and always in locality E. The development of Idotea is direct. The eggs of Idotea are retained in the marsupium where they are fertilized, later hatched and released as juveniles. The marsupial stages are:

- Stage 1: In this stage the eggs are surrounded by an egg membrane. Eggs are spherical with centrally placed yolk. At the rupture of the membrane the egg enters the second stage.
- Stage 2: Embryo is enclosed in the embryonic membrane, the rupture of which ends the second stage.
- Stage 3: Fully developed embryo with appendages but no setae on pereopods.
- Stage 4: This stage is synonymous with the free-living instar which upon release are c. 1.8 - 2.0 mm.

3.2.1. Number of eggs per female

The number of eggs produced by a female was found to be strongly correlated to the size of the female (Fig. 7). These correlations existed between and within species, which means that the number of eggs carried by a female may be a linear function of the female volume.

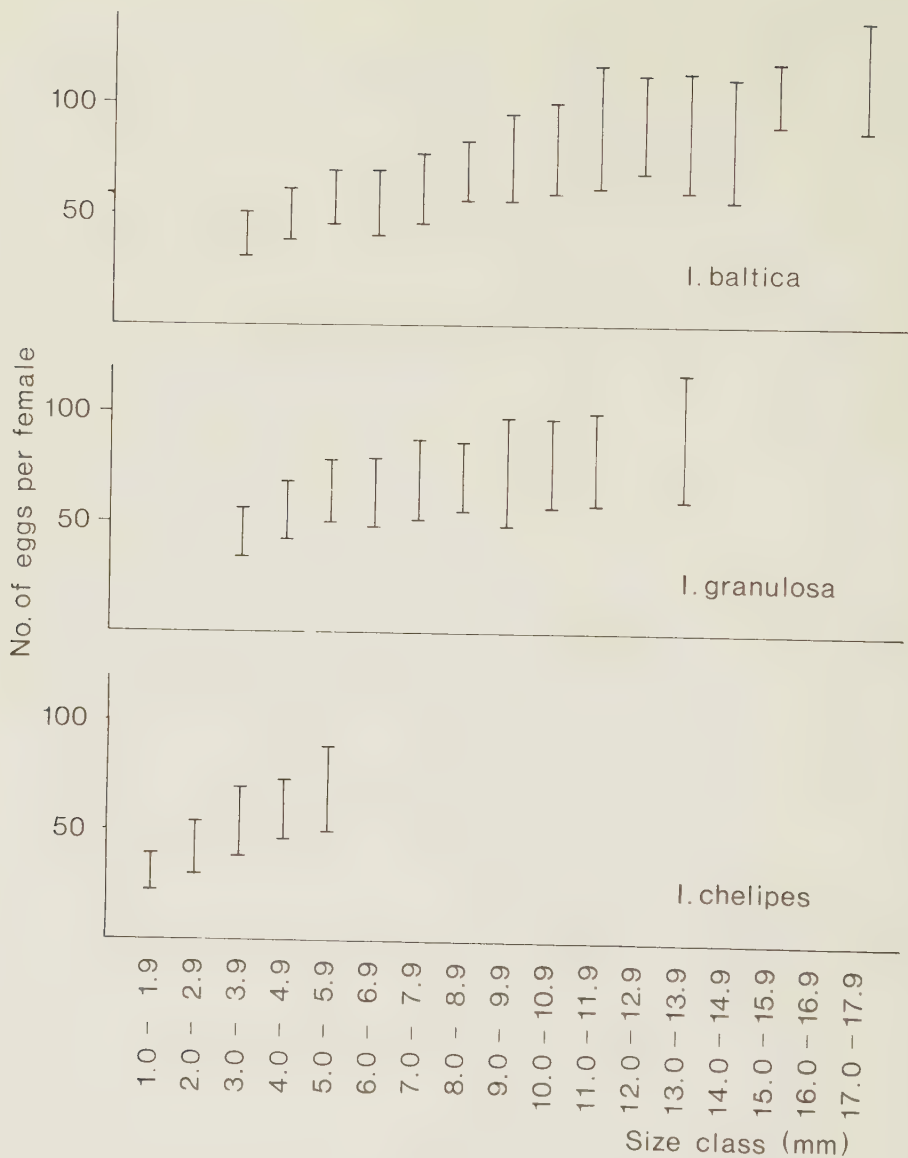


Fig. 7. Relation between body length and fecundity ($\pm$ S.D.) of *Idotea baltica*, *I. chelipes* and *I. granulosa* during the reproductive period in 1977.

The number of eggs increases as the female grows (Fig. 7). Fecundity varied according to the species. For example, the highest number of eggs recorded for the three species were 138 for I. baltica, 116 for I. granulosa and 95 for I. chelipes (Tab. 2). Nevertheless, the number of eggs per mg body weight of a female was highest in I. chelipes and least in I. baltica (Fig. 7).

This is apparent when comparing the weight classes that overlap in the three species, e.g. 3.00 - 3.99 mg, i.e. I. chelipes > I. granulosa > I. baltica. The average fecundity in the 3.00 - 3.99 mg class were 40 eggs/? in I. baltica, 45 eggs/? in I. granulosa and 54 eggs/? in I. chelipes. The tendency was the same in also the next class where comparison was possible.

A.K. Ms 3

Table 2. Maximum and minimum sizes of Idotea species in southern Baltic sampled 1976-1977.

Species	Max. sizes (mm)		Max. brood size	Dry weights (mg)	Size of breeders (mm)		Min. sizes (mm) of breeders	Min. size at sex (mm) differentiation
					1976	1977		
<u>I. baltica</u>	22.0	16.0	138	11.8	11.8	12.0	7.6 - 8.0	5.0 - 5.5
<u>I. granulosa</u>	18.0	14.5	116	13.7	11.3	11.8	7.1 - 7.5	4.5 - 5.0
<u>I. chelipes</u>	17.0	11.0	95	3.0	8.8	8.6	6.0 - 6.2	4.0 - 4.5

The mean number of eggs produced by I. baltica in the 13.00 - 13.99 class was 87 but any number from 66-117 may be found in any individual female. The number of eggs per female decreased all through the breeding season (Fig. 8). Thus, it seems as if females had higher fecundity when producing the first cohort than the second. However, also in I. granulosa, despite of the fact that it had only one cohort, the fecundity seemed lower at the end of its breeding season.

3.2.2. Females participating in reproduction

Tab. 1 shows the percentages of females that actively participated in the reproduction. A large percentage of female I. baltica reproduced in June when the percentage rose suddenly from 18.1 % (May) to 74.8 % and stayed at 73.8 % in July. Slightly more than half of the females reproduced in August, after which the percentage declined. In I. chelipes about 75 % of the adult females were ovigerous in June. The highest percentage of ovigerous females occurred in August (83.1 %). In I. granulosa, May and June were the only months in which females reproduced. By July, only very

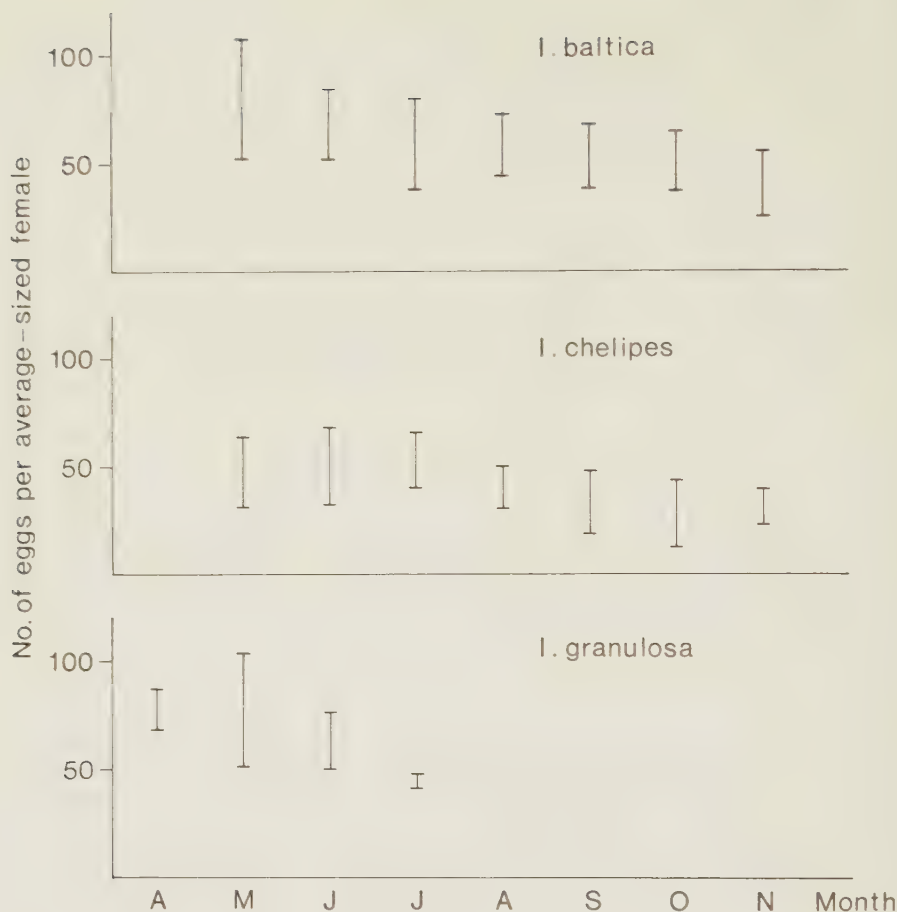


Fig. 8. Relative fecundity (eggs/average-sized female) of *Idotea baltica*, *I. chelipes* and *I. granulosa* during the reproductive period in 1977.

few females were found with embryos or eggs.

Considering separate localities (Fig. 9A), there was a remarkable asynchrony between locs A and C in *I. chelipes*. Thus, in loc. A there was a strong reproduction in May (> 90 % of the females reproduced) and a weaker in July (c. 50 %) while the reverse was found in loc. C: May 35 % females reproducing and July 95 %.

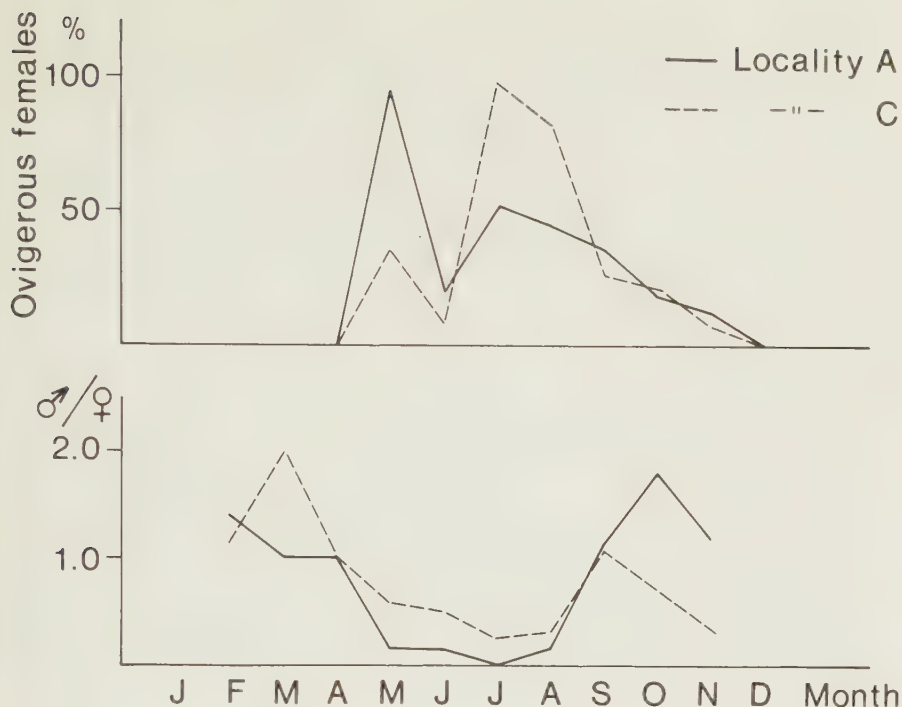


Fig. 9. Percent ovigerous female *Idotea chelipes* (above) in locality A and C during the reproductive period in 1977. Below: Sex ratio (♂/♀) in *I. chelipes* during the same period.

Tab. 2 shows the maximum and minimum sizes of the three species participating in reproduction.

3.2.3. Loss of eggs during marsupial phase

Separate counts of eggs and embryos of *I. baltica* and *I. chelipes* in each mm class were compared (Tab. 3). Females generally carried less embryos than eggs. In the 11-12 mm class in June this difference was significant ($p < 0.01$) for *I. baltica*. In *I. chelipes* significant difference was found between eggs and embryos in the 10-11 mm class ($p < 0.01$) and in the 8-9 mm class in the June samples ($p < 0.01$). To conclude, in 5 out of 8 cases *I. baltica* had fewer embryos than eggs and in *I. chelipes* in 9 out of 12 cases. All these differences suggest that a certain amount of eggs are lost during incubation.

During the years of collection, it was observed that a large percentage of egg-carrying females were infected with fungi (Tab. 1). The fungi were never found in females with embryos. The percentage of infestation increased with increased percentage of ovigerous females. In I. baltica, 17.9 % of all egg-carrying females were infected in June and 31.6 % in July, almost one-third of all ovigerous females. This means that large percentage of eggs are already destroyed during incubation. In I. chelipes, 32.8 % of all ovigerous females were infected in September and 15.4 % in I. granulosa in June.

3.3. Sex ratio

The sizes at which sexual differentiation was possible differed in the three species (Tab. 2). Males of I. baltica could be differentiated at 5.0 - 5.5 mm, 4.5 - 5.0 mm in I. granulosa and 4.0 - 4.5 mm in I. chelipes. Males made up over half of the adult population before and after the breeding season.

Fig. 9B shows comparison between two localities, A and C, for I. chelipes in 1977. The decline in sex ratio indicate that males die off before females during the breeding season.

3.4. Biometrics

3.4.1. Length-antennule segment

A relationship was observed between the body length (Y) and antennule segments (X) and the correlation for both males and females of each species have been calculated. Comparison between both sexes by ANOVA showed significant differences ($p < 0.05$). Hence, males and females were treated separately. The relationship between numbers of antennal segments and body length for I. baltica was $Y = 0.53X + 3.45$, $r = 0.71$ in males and $Y = 0.72X + 0.72$, $r = 0.89$ in females. The equations show that the length of the animal increases 0.53 times in the males and 0.72 times in the females each time a new segment is added.

In I. chelipes, the relationship was expressed by the formula $Y = 0.74X + 1.48$, $r = 0.90$ in males and $Y = 0.89X + 0.30$, $r = 0.81$ in females. The increase in body length relative to antennule segment was higher in the female than males. In I. granulosa, $Y = 0.47X + 3.07$, $r = 0.76$ in males and $Y = 0.23X + 5.41$, $r = 0.36$ in the females. The relationship between the two variables was less in the females of I. granulosa.

Table 3. Comparison between number of eggs and embryos in marsupia of
I. baltica and I. chelipes of different length-classes in 1977.

L e n g t h c l a s s										
<u>I. baltica</u>										
Month	11-12 mm $\bar{x}$		12-13 mm $\bar{x}$		13-14 mm $\bar{x}$		14-15 mm $\bar{x}$		15-16 mm $\bar{x}$	
MAY	egg	28-69 n=6	47	23-84 n=11	59	27-103 n=4	71	41-120 n=8	85	117 n=1
	embryo	55-60 n=2	58	59-87 n=4	70	59-127 n=11	85	45-106 n=2	76	90-137 n=3
JUN	egg	35-76 n=8	62	53-79 n=6	70	68-107 n=3	85	95-138 n=3	112	-
	embryo	30-80 n=24	52	42-89 n=23	64	33-101 n=11	71	59-86 n=7	76	-
<u>I. chelipes</u>										
	7-8 mm	$\bar{x}$	8-9 mm	$\bar{x}$	9-10 mm	$\bar{x}$	10-11 mm	$\bar{x}$		
JUN	egg	27-41 n=2	34	33-51 n=6	42	20-79 n=16	50	45-90 n=9	65	
	embryo	39 n=1		24-49 n=20	37	25-60 n=13	45	55-68 n=5	61	
JUL	egg	23-41 n=4	33	40-56 n=6	49	34-95 n=10	57	53.00 n=1		
	embryo	-	n=5	21-38 n=8	31	34-63 n=4	54	55-72 n=4	64	
AUG	egg	22-55 n=5	32	21-53 n=11	43	31-60 n=9	46	88.00 n=1		
	embryo	16-32 n=11	25	23-57 n=19	36	39-64 n=7	48	-		
SEP	egg	17-31 n=4	26	29-47 n=3	38	35-71 n=4	52	-		
	embryo	17-38 n=2	28	31-42 n=4	37	35-47 n=3	39	-		

4. Discussion

The Idotea species' seasonal fluctuations in southern Baltic resemble those described by Jazdzewski (1970), Betz (1974) and Salemaa (1979). Changes in abundance during the winter months were found to be similar to the fluctuations reported from England (Homes 1939). Several hours of search in the sea-weeds could only give an occasional catch of 1-2 individuals. The rarity of I. granulosa along the Swedish coast is not of recent occurrence (Forsman 1956). Its low density even in lotic areas had been attributed to its poor competitive ability when co-existing with the other species. This could have contributed to its earlier breeding period as a means of avoiding competitive pressures.

The situation was different in northern Baltic where Haage (1975) registered slight increase in the I. baltica population during the winter. He accounts this increase to the ice-cover equalizing the effect of turbulence on exposed localities.

Maximum sizes of Idotea species from southern Baltic are slightly larger than those examined by Muus (1967), Sywula (1964a) and Salemaa (1979). For example, Sywula gave 20.5 mm and 13.1 mm as maximum sizes for males and females, respectively, of I. baltica; 14.4 mm for males of I. granulosa and 10.9 mm for females while I. chelipes had 13.9 mm for males and 10.1 mm for females. Those from Bay of Puck (Jazdzewski 1970) corresponded to the sizes in my collections. However, those of I. baltica from North America (Strong 1978) are larger than those examined by me.

Fecundity was a linear function of the volume of the female in many Crustaceans (Jensen 1956, 1958, Kinne 1961, Schütz 1963). However, this relationship is not applicable at all times in what Kinne (1961) called "senile females", i.e. females reaching their maximum physiological age. Such females produced fewer eggs. Jensen (1958) showed that the absolute number of eggs was dependent on external factors whereas the relative number depended on the volume of the female. Such relationship between the brood size and the volume of the female is found in my samples depending also on the season, age and size of the female. Furthermore, females in more saline locality A tended to carry slightly higher number of eggs than those from less saline locality C. Maximum eggs recorded from the Baltic in I. baltica is 138 whereas from North America the maximum brood size encountered was 567 in I. baltica (Strong 1978).

The duration of breeding season in the Idotea species varies according to the sampling area. I. emarginata was found to breed throughout the year at Port Erin from the Isle of Man (Naylor 1955d). Labourg (1971) working with I. chelipes in France found four cohorts. Sheader (1977) showed I. pelagica to have restricted breeding season between April to August with juveniles released between June and September. In the Baltic species, Betz (1974) reported from May to August for I. chelipes and Jazdzewski (1970) had from May to November for I. chelipes with two hatching intensities. My samples from southern Baltic show I. granulosa having its breeding season from April to July with one generation and May to November for both I. chelipes and I. baltica with two release of juveniles in June/July and September in I. baltica and June and September in I. chelipes.

Reduction in the number of eggs has been observed in many isopods. Such a loss has been described in Asellus aquaticus and I. chelipes (Jancke 1926), I. chelipes (Howes 1939, Betz 1974), Sphaeroma hookeri (Kinne 1954), Asellus aquaticus (Steel 1961), I. baltica, I. granulosa and I. chelipes (Salemaa 1979). Similar reduction in the eggs existed in my samples. The method of sampling did not contribute to the reduction. However, the eggs might perhaps have leaked out of the marsupium for lack of space as maintained by Jancke (1926), although Kjennerud (1950) and Strong (1978) both working with I. neglecta and I. baltica, respectively, did not observe any egg reduction in their samples. Kjennerud (op.cit.) states that lack of space was not a sufficient reason for the reduction since the size of the marsupium increases, the oostegites separating as the embryos develop. This enlargement of the brood pouch was also confirmed by Strong (1978).

Different stages of development in the marsupium had been reported for I. chelipes (Homes 1939). While majority were ready to hatch, three or four may be at an earlier stage of development, which he thought contributed to the low number of eggs. I have observed similar developments in I. chelipes in southern Baltic. On the 15 June 1977 from locality C, a 10.0 mm female of I. chelipes had 35 eggs of stage 1 and 10 embryos of stage 2.

Changes within the sex ratio as observed from the field can be influenced by ecological factors, such as mortality and migration. Haage (1975) found evident upward migration in the I. chelipes population with a decrease in the population. Anyway, migra-

tion is thought to have nutritional cause (Jansson 1969). Reduction in the males after copulation is more likely associated with mortality than nutritional cause. The older females probably die off after releasing their juveniles.

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FOOD AND SUBSTRATE PREFERENCE OF THREE CO-EXISTING SPECIES
OF IDOTEA (CRUSTACEA, ISOPODA). A LABORATORY INVESTIGATION.

Paper C

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Abstract

Preference of algae was examined for Idotea baltica, I. granulosa and I. chelipes and relative feeding rates for I. baltica on six marine algal species common in the southern Baltic. Ingestion rates increased with increasing animal size and was highest when Fucus vesiculosus was provided as food and lowest for Ulva lactuca. In preference experiments the species of Idotea were studied alone or in combinations. All species preferred Ruppia spiralis when alone. However, when I. granulosa was kept together with the other two species it changed preference to either Chorda or Fucus indicating a lower competitive ability.

1. Introduction

In terms of food, preference is often difficult to define, since the factors involved are complex and interrelated. Most often preference is ambiguously used for availability. In the temperate zone where large temperature fluctuations affect the growth of the different algal species forming important food resources for species of Idotea, the occurrence of a certain sea-weed in a particular season surely influences the food preference of many herbivores. Thus, Fucus is found along the South Swedish coasts throughout the year, while Cladophora and Enteromorpha are mostly not observed during the winter. As for many aquatic invertebrates, the diet of Idotea species (Crustacea, Isopoda) is poorly known and has been discussed for many years. However, investigations have shown that they are mainly omnivorous (Naylor 1955a, Cruz 1960, 1963, Sywula 1964).

Energy utilization and food preference have been studied in a number of marine invertebrate herbivores (see e.g. Strong and Daborn 1979, Nicotri 1980). Preference for a particular sea-weed may be affected by the stage of growth (Naylor 1955b, Jansson 1967) or it may be influenced by the sensory, nutritional and mechanical properties (Westoby 1974). While the chemical composition of sea-weeds is known to fluctuate (Black 1949, Macpherson and Young 1952, Wort 1955), these plants have developed toxic chemical substances that give them some degree of protection against predation (e.g. Levin 1971, 1976).

The Idotea species described in this paper frequently occur on sea-weeds, which often form patches on sandy bottoms. The co-existence of three Idotea species on a single plant implies an elaborate partitioning of resources to minimize competition. The present

study is focused on the feeding of I. baltica on six algal species and the food and substrate preference of I. baltica, I. chelipes and I. granulosa when appearing as single species or together with one or both of the other two.

2. Properties governing food and substrate preferences

Besides the nutritional values, preference can be influenced by the mechanical and sensory properties of an alga (Westoby 1974). In areas with strong water movements, an alga must be firmly attached to provide shelter for an animal. This might possibly have contributed to the high frequency of Idotea on Fucus in the sampling sites of stronger water movement. Thus, green algae, i.e. Ulva or Cladophora, floating freely near water surface do not provide a good shelter. However, in areas with weaker water movement and no permanent Fucus or Ulva vegetation, most isopods collected were on Ruppia. Besides being food resources the ability of an alga to provide a hiding place against predators, a spawning place and a suitable place to avoid stronger water movement influence the isopod's preference. Nicotri (1980) found that I. baltica was attracted to large, tough, branched algae (perennials), while Amphithoe valida preferred softer, filamentous or bladed algae (ephemerals) and annuals.

Also other properties of an alga, such as palatability, appearance and texture might be important for preference. Nicotri (1980) further found that when Idotea species could choose between plastic plants and unattractive live species, they preferred the former. This indicated that these isopods responded to algal morphology rather than to food value. Food choice can also be related to body size, which is illustrated in I. granulosa, whose juveniles live on Cladophora, which is tender, while the mature specimens prefer the harder fucoids (Naylor 1955b, Jansson 1967).

3. Method

The Idotea species were collected along the coast of the Falsterbo peninsula in southernmost Sweden (Fig. 1). Predominating sea-weeds in the localities sampled were Cladophora rupestris, Chorda filum, Enteromorpha intestinalis, Fucus vesiculosus, Ruppia spiralis and Ulva lactuca. These algae grow dense during the summer and autumn coinciding with the release of juvenile isopods. Some algal species completely disappear along the shores during the winter, i.e. Enteromorpha intestinalis, while others like Fucus vesiculosus are

found throughout the year.



Fig. 1. Location of study area.

Two methods were employed in studying algae preference in Idotea species:

(1) The relative feeding rates were obtained by providing specimens of I. baltica one type of alga as food at a time. Four different size classes were considered, viz. 0-5, 6-10, 11-15 and 16-20 mm. The algae were weighed damp dry and placed in two-liter containers with 10.0 ‰ aerated seawater in a thermo-constant room ($12.5 \pm 0.5^{\circ}\text{C}$) supplied with two neon lights. Five isopods of each size class, starved for 24 h were added to each container and two replicates per alga were run. After 72 h, the animals were removed and the remaining algae damp dried and weighed. The difference between the weights of the algae before and after the experiment was corrected for weight loss of a control group in seawater kept for the same period but without animals, thus obtaining the weight actually ingested.

(2) Pieces of all six species of algae were placed in a sorting bowl and 10.0 ‰ seawater added just enough to cover them. Isopods starved for 24 h were introduced into the bowl and their occurrence on the different algal species were noted every half hour for eight hours. After each checking the animals were released again in the center of the bowl after the positions of the algae were rotated

about 90° so as not to make the animals accustomed to a particular alga in a constant position. The experiment was run with seven replicates with 30 animals per replicate (with disregard to sex and colour) released in each bowl, either as all of a single species or 15 of each species of two or 10 of each species of three.

The term 'preference' is used for an alga which was regularly visited by a large percentage of a certain Idotea species while 'relative feeding rates' merely means the difference in damp-dry weights of the algal species before and after the experiment. The material ingested might to some extent consist of particular luxuriant epiphytic growth associated with a certain algal species and to a certain extent of the alga itself. I did not discriminate between these two types of food in this study.

4. Results

4.1. Preference of algae

Certain algae were generally more preferred than others (Fig. 3). Generally, Ruppia was preferred above all other algae by all three species of Idotea (Fig. 3A-C). However, I. granulosa combined with I. baltica shifted its preference to Chorda (Fig. 3F). while I. baltica still preferred Ruppia (Fig. 3G). Further, when I. granulosa was combined with I. chelipes it preferred Fucus (Fig. 3I), while I. chelipes still preferred Ruppia (Fig. 3H).

When all three species were kept together I. granulosa again shifted to Fucus (Fig. 3L).

4.2. Ingestion rate of algae

In all size classes of I. baltica the tough Fucus was much more consumed than any other presented alga. Ingestion rate increased with increasing size, the larger the size of the Isopod, the greater was the amount eaten. Ulva lactuca, on the other hand, was the distinctly least consumed alga. The group consisting of Cladophora, Chorda, Ruppia and Enteromorpha were roughly equally preferred. The small preference differences were consistent all through the four size classes. (Fig. 2).

Ingestion rates and preference for I. baltica are compared in Tab. 1. The two experiment series show no complete agreement, but Ruppia and Fucus are most preferred and ingested in the two series.

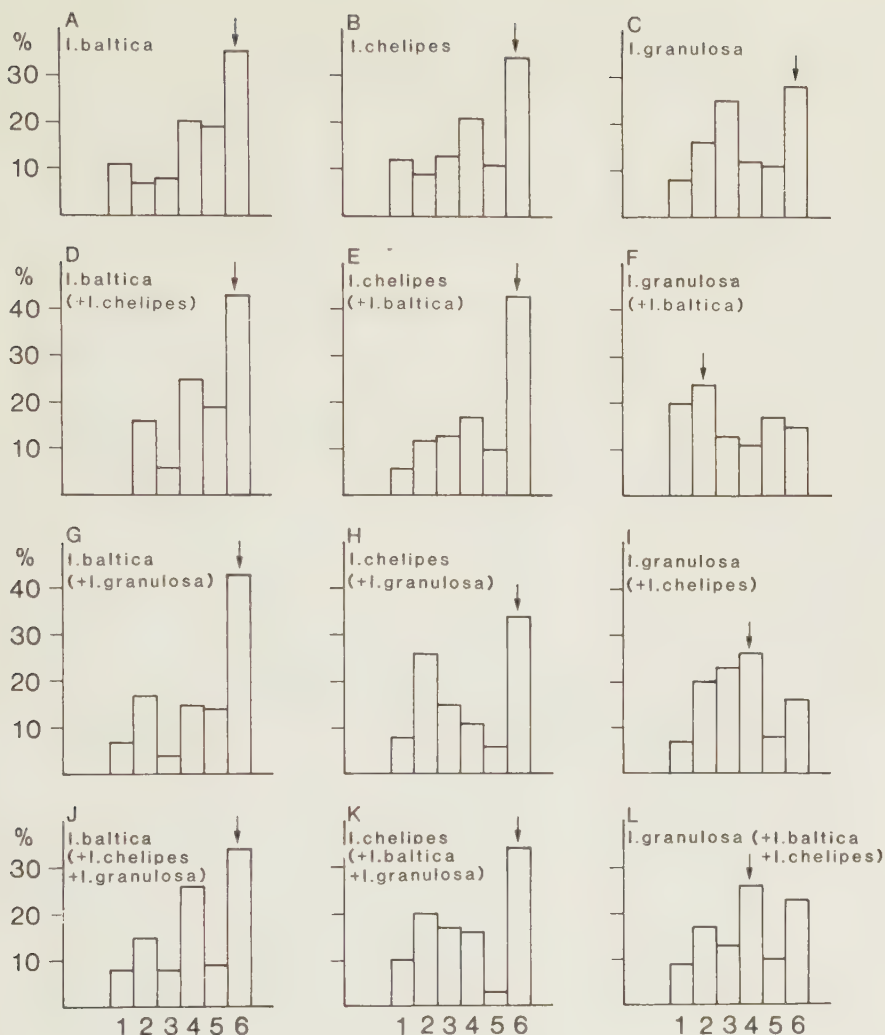


Fig. 3. Preference experiment showing the relative occurrence of *Idotea baltica*, *I. granulosa* and *I. chelipes* on different algal species in the laboratory. The preference is shown for the different species either alone or in combination with one or both of the other two species (in parenthesis). Six species of algae were used, viz., (1) *Cladophora rupestris*, (2) *Chorda filum*, (3) *Enteromorpha intestinalis*, (4) *Fucus vesiculosus*, (5) *Ulva lactuca* and (6) *Ruppia spiralis*.

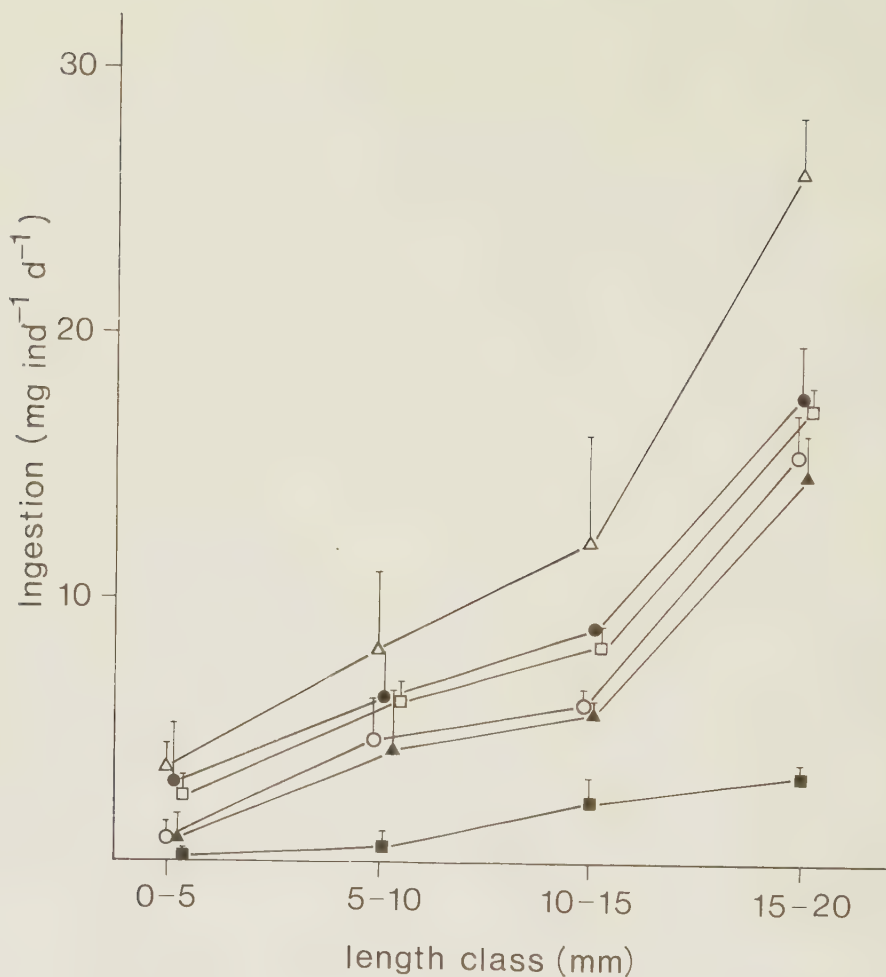


Fig. 2. Relative feeding rates ($\text{mg ind}^{-1} \text{d}^{-1}$) of *Idotea baltica* separated into four size classes. Six species of algae were used as food, viz. *Fucus vesiculosus* Δ , *Cladophora rupestris* $\blacktriangle$, *Chorda filum* $\circ$, *Ruppia spiralis* $\bullet$, *Enteromorpha intestinalis* $\square$, and *Ulva lactuca* $\blacksquare$.

Tab. 1. Preference and ingestion rates of Idotea baltica with different algal species as food.

Algae	Preference (%)	rank	Ingestion rate (mg algae, ind ⁻¹ day ⁻¹)	rank
<u>Enteromorpha intestinalis</u>	7.9	5	8.3	5
<u>Ulva lactuca</u>	19.3	3	1.6	6
<u>Cladophora rupestris</u>	11.0	4	6.4	4
<u>Fucus vesiculosus</u>	20.5	2	12.5	1
<u>Chorda filum</u>	6.7	6	7.1	4
<u>Ruppia spiralis</u>	34.7	1	9.0	2

5. Discussion

This paper deals with food and substrate preferences of three Idotea species as well as the feeding of I. baltica, the most common species around the Falsterbo peninsula. Of the two methods used, viz. the preference study and the ingestion rate experiment the first one includes both the organism's substrate and food choice, while the latter only considers the food choice. This is illustrated by Tab. 1. The two most visited algae (Fucus and Ruppia) were also highly utilized as food. Thus, these two algae seems to provide both food and shelter. On the other hand Ulva and Cladophora were fed upon to a much lower extent than expected with regard to the preference experiment. This might be explained by a lower energy content in these species and/or some secondary substances resulting in a lower palatability (Ogden 1976). However, these algae might be used for shelter and hence constitute an important patch in the natural heterogeneous habitat.

In the ingestion experiment each size class was studied separately (Fig. 2). All size classes had highest ingestion of Fucus. The other 5 algal species tested were all ingested in lower but agreeing proportions for all Isopod size classes. As all size classes were studied separately the results reflect the true food preference for each size class. In a free-living population it is reasonable to believe that interference between individuals of different size may change the food preference for the smallest size classes.

In the food and substrate preference experiments the three species of Idotea had roughly the same preference with a dominance for Ruppia. When coexisting with one or two other species I. baltica and I. chelipes still maintained their preference for Ruppia. I. granulosa, on the other hand, with a body size in between I.

baltica and I. chelipes, showed a niche shift from Ruppia to either Fucus or Chorda when kept with chelipes or baltica or both.

In all species combinations examined I. granulosa changed its food niche from Ruppia to some other alga, strongly indicating a lower competitive ability. This is supported by their dominant occurrence in exposed coastal habitats in the southern Baltic.

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COLOUR POLYMORHPISM IN IDOTEA BALTICA (CRUSTACEA, ISOPODA)

IN THE SOUTHERN BALTIC

Paper D

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Abstract

The occurrence of different colour phenotypes of Idotea baltica (Crustacea) in five localities along the Swedish south coast was investigated. Idoteas belonging to the phenotype uniformis were most frequent while lineata and pseudolineata were rare. Males dominated in all phenotypes except in albafusca and the black morph of uniformis where females were dominant.

The phenotypic composition of the populations was relatively constant over the three years studied. A positive correlation between phenotypic diversity and habitat diversity was found. Further, in localities where brown algae dominated, brown morphs were frequent and where green algae dominated green morphs were common. It is concluded that selected predation may affect the phenotypic composition of a population so that the least apparent phenotype is favoured.

1. Introduction

Idotea baltica (Pallas) is common in the southern Baltic. The species is known for its body colour polymorphism described by Tinturier-Hamelin (1963a, b) and controlled by the genetic composition of the populations, influenced by e.g. selection, changes in the environment or directly related to or modified by biotic factors (Lee 1966a, b, 1967).

Seasonal and geographical variabilities in the colour phenotypes of I. baltica have been the subject of recent studies in the northern Baltic (Salemaa 1978, 1979). Polymorphism in I. baltica is regarded as "balanced". Such balanced polymorphism is maintained by apostatic selection (Clarke 1962, 1964, Cook and Miller 1977).

The present study describes the frequency of six phenotypes of I. baltica at five localities in the southern Baltic and discusses fluctuations and their mechanisms in relation to selected environmental factors.

2. Method

2.1. Collection, measurements and calculations

The study is based on 6785 I. baltica individuals collected from five localities in 1975 through 1977. The localities are classified as sheltered (locality A) and exposed (localities B to E) (Fig. 1). Sampling, preservation, sex determination, life cycle

and fecundity of this species have been described earlier (Korheina, paper B). Each animal was scored for sex and body colour patterns for colour phenotypes. As juveniles are completely colourless, only adults were examined.

The vegetation in the sampling sites was noted. Each sampling site was mapped by marking an area of 25 x 20 m, within which five random samples 25 x 25 cm were taken. The algal species occurring in each sample were sorted out in groups. These groups were dried separately at 60° C for 24 h and weighed.

The phenotypic diversity index (H') was compared with Hutchinson (1970) test, expressed by Shannon diversity index (Pielou 1966a, b).



Fig. 1. Sampling localities in southern Baltic.

2.2. Phenotypes

The colouration of Idotea species depends on occurrence, distribution and contraction or expansion of chromatophores (Sunesson 1947, Highman and Hill 1969). The interchromatophoral spaces can be colourless, light orange or green. Chromatophores are more plentiful in females than in males. Males are larger and less pigmented than females.

Previous studies on chromatophore patterns in I. baltica have indicated several phenotypes. Tinturier-Hamelin (1963a, b) and Salemaa (1978, 1979) identified six and four colour phenotypes, respectively, occurring in a number of combinations. In my collection from the southern Baltic, six major phenotypes were identified. These include uniformis, bilineata, maculata, albafusca, lineata and pseudolineata.

The detailed examination of the material with respect to albafusca and flavafusca phenotypes (Tinturier-Hamelin op.cit.) showed that the differences between the two groups were ill-defined in the Baltic species and therefore did not warrant separate phenotypes. As a result, both were classified under albafusca. This was also confirmed for the northern Baltic (Salemaa op.cit.).

The genetic mechanism responsible for the colour polymorphism in Idotea baltica was described in detail by Tinturier-Hamelin (1963a).

2.2.1. Bilineata (Fig. 2A)

The light lateral lines are symmetrically placed on both sides of the body extending from the first thoracic segment to mid-telson. The combination, bilineata-lineata, has in addition to the two lateral lines also a mid-dorsal band found in lineata.

2.2.2. Uniformis (Fig. 2B, G, R)

Uniformis are of three types or morphs (brown, black and green). The black specimens have lost the power of contracting or expanding the chromatophores on a black background in light. Their chromatophores are in permanent state of expansion (Salemaa 1978). In green (Fig. 2R) and brown (Fig. 2B) specimens, the pigments of the chromatophores when contracted give a mottled appearance.

2.2.3. Albafusca (Fig. 2C)

This phenotype is characterized by a distinct mixture of black and light patches. The light areas consisted of four laterally symmetrical patches on each side of the body, usually the first patch on first or second thoracic segment, the second patch on the 4 - 5th thoracic segment, the third patch on the first two somites of pleon and the last patch on the telson. The size of the patches varies individually. Flavafusca (Fig. 2H) is described by Tinturier-Hamelin (1963a) as being similar to albafusca but without leucophores.

2.2.4. Maculata (Fig. 2D)

These specimens are marbled, marked with indefinite mottles. The phenotype exhibits great variation.

2.2.5. Pseudolineata (Fig. 2E)

This type is similar to lineata (Fig. 2F), but the mid-dorsal line or band ends abruptly after the second somite of pleon.

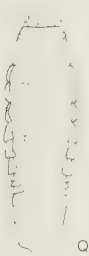
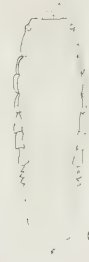
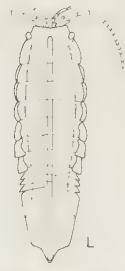
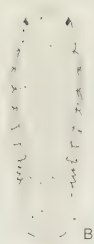
2.2.6. Lineata (Fig. 2F)

Like the preceding phenotype. lineata has a narrow mid-dorsal band of leucophores which is normally of equal width throughout its length. It runs from the cephalon to the end of telson. Lineata and pseudolineata were not represented in the collections from the northern Baltic (Salemaa 1978, 1979).

2.2.7. Combinations of phenotypes

The combinations of the six major phenotypes (Figs 2 I-S) included bilineata-maculata (Fig. 2I), bilineata-lineata-albafusca (Figs 2 J and S), bilineata-lineata-maculata (Fig. 2K), bilineata-lineata (Fig. 2L), pseudolineata-albafusca (Fig. 2M), maculata-lineata (Fig. 2N), maculata-albafusca (Fig. 2O), pseudolineata-maculata (Fig. 2P), pseudolineata-maculata-albafusca (Fig. 2Q).

Fig. 2. Diagrammatic drawings of phenotypes and morphs of I. baltica in southern Baltic. A: bilineata, B, G, R: uniformis (brown, black, green), C: albafusca, D: maculata, E: pseudolineata, F: lineata, H: flavafusca, I: bilineata-maculata, J, S: bilineata-lineata-albafusca, K: bilineata-lineata-maculata, L: bilineata-lineata, M: pseudolineata-albafusca, N: maculata-lineata, O: maculata-albafusca, P: pseudolineata-maculata, Q: pseudolineata-maculata-albafusca.



3. Results

3.1. Vegetation

In locality A Ruppia spiralis was the dominant plant species, followed by Enteromorpha intestinalis. Two Fucus species were abundant in the other four localities. Fucus was transported to locality A from other areas floating in the water, i.e. they were not attached to stones or rocks as in other localities. Ulva lactuca was found in all localities but was not attached. Ruppia spiralis, Enteromorpha intestinalis, Ulva lactuca, Zostera marina and Ceramium rubrum were present in all sampling sites. Cladophora rupestris was not present in samples from localities C and E.

The dry weight averages of vegetation groups sampled in 25 x 25 cm in each locality were used to calculate the habitat diversity indices. The following values were recorded: locality A: 1.97, B: 3.01, C: 2.55, and 2.60 for localities D and E each.

3.2. Local distribution of phenotypes

Fig. 3 shows the frequency of the different phenotypes at each locality. All the six phenotypes were represented at the five sampling sites. Uniformis was by far the most common phenotype and in all sampling sites more than 50 % of all idoteas were of this phenotype. Maculata was the second most recorded one in four out of five localities. Lineata was the totally least frequent phenotype.

As the samples were not quantitative, the relative frequency of each phenotype has been calculated, i.e. as if the samples had been equal-sized in all localities. As a result, different distribution patterns may be distinguished (Fig. 4). Thus, the most frequent uniformis, was the most evenly distributed phenotype with a steady frequency per locality of around 20 %. Bilineata and lineata showed quite a different, but agreeing, pattern with a pronounced peak in C, with 35 and 45 %, respectively. They were both second in numbers in locality B. Albafusca and pseudolineata on the other hand, had their lowest frequency in C. Maculata had a frequency of 20 - 25 % in localities B through E, but a very low value was noted in the sheltered locality A (3 %).

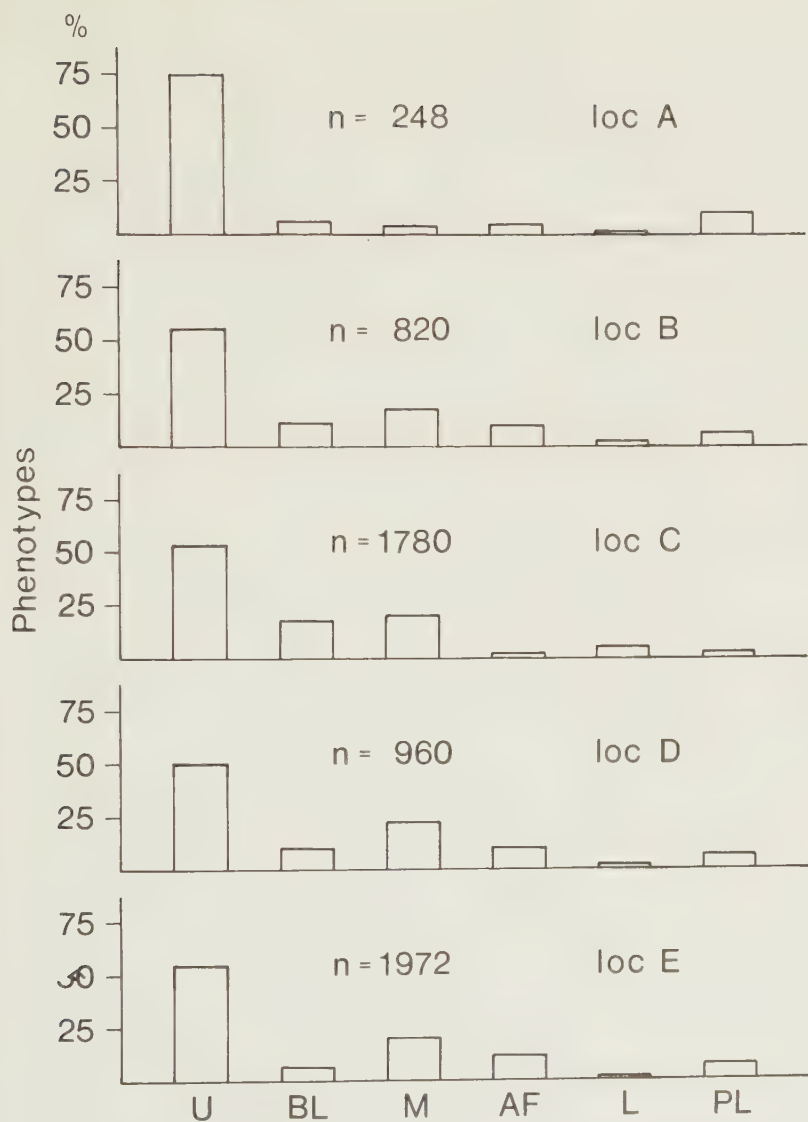


Fig. 3. Occurrence of phenotypes of *Idotea baltica* in different localities. U = uniformis, BL = bilineata, M = maculata, AF = albafusca, L = lineata, PL = pseudolineata.

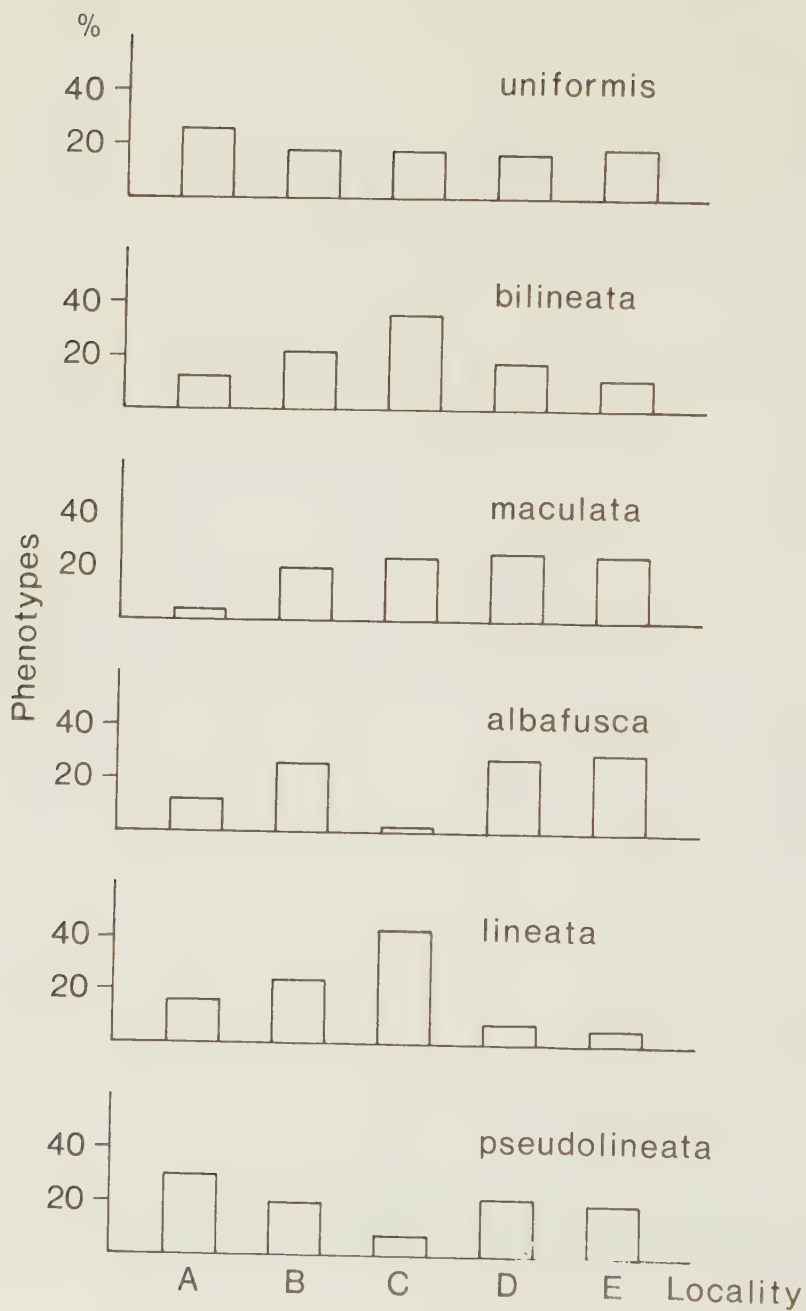


Fig. 4. Calculated relative occurrence of phenotypes of *Idotea baltica* in different localities.

3.3. Sex ratio

Tab. 1 shows the number of males and females as well as the sex ratio, expressed as number of males per female of the different phenotypes in each locality. The sex ratios of the different phenotypes varied a great deal between localities, but there was a tendency in some cases for one sex to dominate. Thus, in lineata and pseudolineata males were dominating, especially in the latter, with a mean sex ratio of 8.50. Still more pronounced, however, but in the other direction, was albafusca with a ratio of 0.11, i.e. a heavy predominance of females. Uniformis, with a mean ratio of 1.81, was the only phenotype collected in great numbers in all localities, and the highest sex ratio noted for that phenotype (4.11) was in the only sheltered locality A. Males were generally more abundant in locality A than in other areas.

3.4. Seasonal variations in phenotype sex-ratio and frequencies of phenotypes and colour morphs

In all seasons and years uniformis was by far the most common phenotypes, with a frequency of 45 - 75 % of the total population in any season (Fig. 5). In spring in all the three years maculata was the second in number. No general trend in changes of the phenotypic frequency between seasons is detectable for the three years, but there is a fairly good agreement in frequency per season between years for some phenotypes.

Because of small samples, meaningful comparisons of the sex ratio variations are possible only for a few phenotypes (Tab. 2). Thus, in the common uniformis there seemed to be an increase of males (higher ratios) in the autumn, probably reflecting a differential mortality. In the extreme albafusca, with a heavy predominance of females, only very small seasonal variations in the sex ratio were noted, but the material was small.

Fig. 6 illustrates the relative occurrence of the three colour morphs of uniformis. All morphs were recorded in great numbers in all seasons but winter. In spring all three morphs were equally abundant. In summer however, the black animals were most common and in autumn and winter there was a dominance of the greens on about 60 %. In all seasons there was a surplus of males of the green morph of uniformis and of females of the black morph (Tab. 3).

Table 1. Number of male and female Idotea baltica and sex-ratio in different localities from 1975 through 1977.

Locality	Sex	U	BL	Phenotypes			L	PL
				M	AF			
A	♂	148	12	8	4		4	16
	♀	36	4	0	8		0	8
	sex ratio (♂/♀)	4.11	12/4*	8/0*	4/8*		4/0*	2.00
B	♂	196	28	124	4		12	52
	♀	236	64	16	80		8	0
	sex ratio (♂/♀)	0.83	0.44	7.75	0.05		1.50	52/0*
C	♂	500	128	236	4		44	40
	♀	448	204	112	16		44	4
	sex ratio (♂/♀)	1.10	0.63	2.11	0.25		1.00	10.0
D	♂	292	40	172	0		8	60
	♀	192	48	40	100		0	8
	sex ratio (♂/♀)	1.52	0.83	4.30	0/100*		8/0	7.50
E	♂	640	88	292	8		12	116
	♀	428	40	120	220		0	8
	Sex ratio (♂/♀)	1.50	2.20	2.43	0.04		12/0*	14.5
Total	♂	1776	296	832	20		80	284
	♀	1340	360	288	424		52	28
	Mean sex ratio (♂/♀)	1.81	1.03	4.15	0.11		1.25	8.50
Number of localities on which mean sex ratio is based		5	4	4	3		2	4

*Numbers < 20 are given only in fractions

U = uniformis, BL = billineata, M = maculata, AF = albafusca, L = lineata, PL = pseudolineata

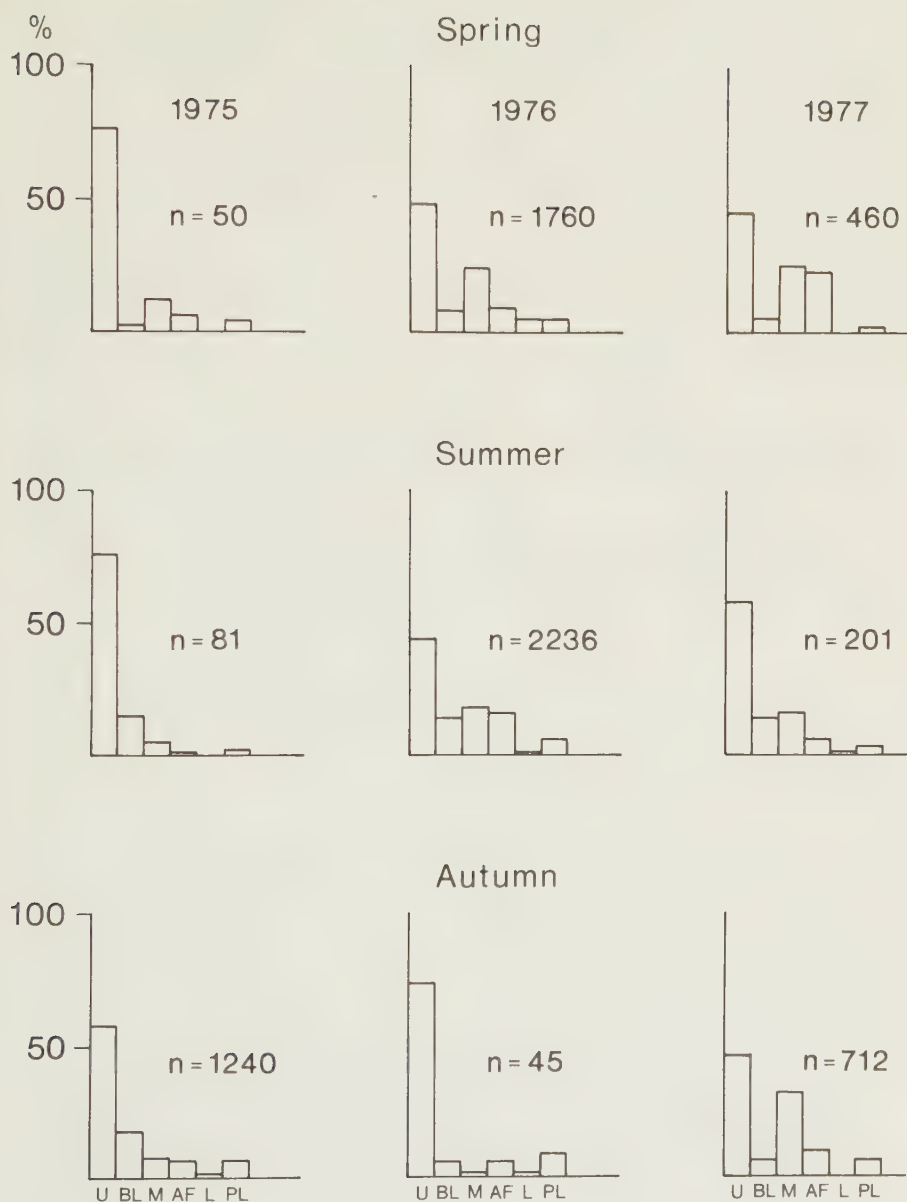


Fig. 5. Seasonal frequencies of *Idotea baltica* phenotypes from 1975 through 1977. Abbreviations as in Fig. 3.

Table 2. Sex ratio (males/females) of four phenotypes in different seasons from 1975 through 1977. (*) Asterisk indicates numbers below 20 which are expressed only in fractions.

Seasons	Phenotypes	U	BL	M	AF
Spring	1975	1.88	-	6/0*	0/2*
	1976	1.37	0.79	4.43	0.24
	1977	0.75	5/4*	1.42	0/21*
Summer	1975	0.92	6/3*	4/2*	0/1*
	1976	9.92	0.53	1.54	0.12
	1977	1.00	3/7*	8/0*	0/5*
Autumn	1975	2.48	0.68	12/5*	3/5*
	1976	10.00	2/1*	1/0*	0/3*
	1977	1.56	4/2*	2.50	0/9*

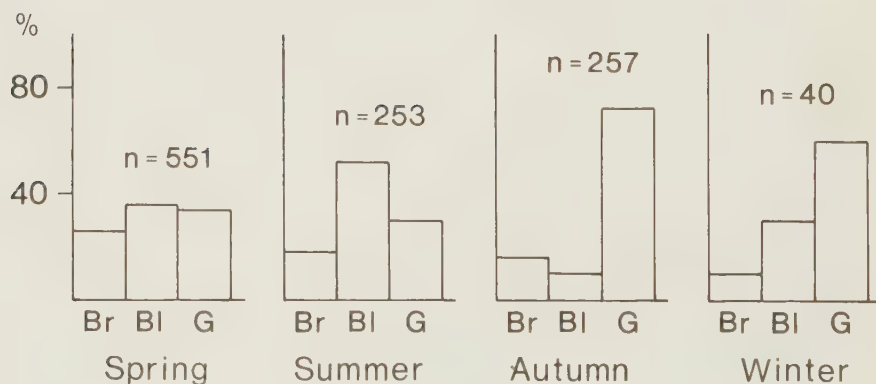


Fig. 6. Seasonal frequencies of colour morphs of uniformis in 1976.
Br = brown, Bl = black, G = green.

Table 3. Sex ratios (males/female) of the different morphs of uniformis in different seasons in 1976. (*) Asterisk indicates numbers below 20 which are expressed only in fractions.

Seasons	M o r p h s		
	Brown	Black	Green
Spring	3.27	0.36	4.80
Summer	0.84	0.02	1.71
Autumn	1.00	0.04	1.43
Winter	2/2*	0/12*	3.80

3.5. Phenotypic diversity and colour morph occurrence in relation to the substrate

The phenotype diversity (H') was higher in the exposed localities (B-E) than in the sheltered one (A) (Tab. 4). Females were most diverse in localities B and C and males in C and D. There was a positive correlation between phenotypic diversity and habitat diversity ($Y = 1.84 - 0.53x$, $r = 0.86$, see sect. 3.1.).

Table 4. Phenotype diversity (H') of males and females in each locality investigated.

Sex	L o c a l i t y				
	A	B	C	D	E
♀	1.48	1.63	1.74	1.83	1.68
♂	1.26	1.88	1.81	1.71	1.71

Fig. 7 shows the relationship between the frequency of the green morphs in the sampling localities and the amount of brown algae (Fucus) on which the Idotea species were sampled. This correlation is highly significant. Thus, in locality A with less Fucus vegetation, higher frequencies of green morphs were recorded whereas in areas with rich Fucus vegetation (C and E) lower frequencies of green morphs were noted. Similar results were also obtained between brown morphs and green algae ($Y = 41.47 - 2.49x$, $r = - 0.61$). Thus, the more Fucus in the habitat, the higher frequency of brown uniformis.

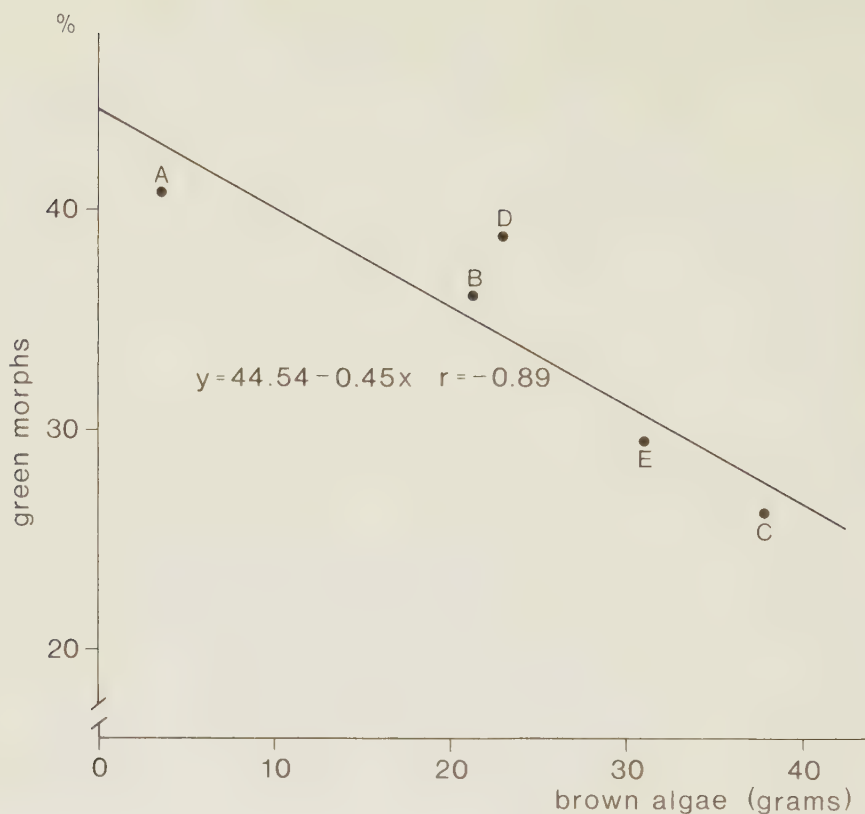


Fig. 7. Relationship between the frequency of green morphs and the amount of brown algae in the sampling localities.

4. Conclusions and discussion

Three species of the genus Idotea occur along the Falsterbo peninsula in southernmost Sweden. Of these I. baltica was the totally most sampled species in all but one of the five localities from 1975 through 1977. Six different phenotypes were distinguished of this species and uniformis was the pronouncedly most common one. In all localities 50 % or more of all individuals were of this phenotype. The others were much less frequent and all had values below 20 %. Furthermore, the six phenotypes were found in about the same proportions in all localities why the differences in the general distribution pattern of the phenotypes were small. Even

between years, and seasons, the phenotypic composition was fairly constant with uniformis as the always dominant one (45 % or more). It should, however, be borne in mind, that uniformis in its turn, is polymorphic as regards the ground colour.

For some phenotypes there was a tendency for one sex to dominate in number. This was especially pronounced in pseudolineata, with a dominance of males, and in albafusca where females heavily dominated. In I. baltica colour polymorphism, e.g. in albafusca, was linked with the female sex, although reversal of sexual phenotypes, very likely of genetic origin, is known to occur in low frequencies of individuals of both sexes (Tinturier-Hamelin 1963a). This sex reversal brought about the occurrence of a male sexual phenotype in a genotypic female and a female sexual phenotype in a genotypic male. The great majority of albafusca in my samples were females, which agrees with their phenotypic determination. However, the low female frequency in maculata strongly suggests sex reversal.

The local densities of the isopods apparently fluctuated during the seasons and so did the sex ratios for some phenotypes. This was found in uniformis where males tended to be most common in the autumn each year. The fluctuations in sex ratios may be related to several factors such as differential migration and longevity, interspecific relationships but also to predation. Thus, the summer decrease of male uniformis could be due to selective fish predation. They are larger than the females, which may make them more easy to detect and attractive, because of their higher nutritional value. The influence of predation as a regulating factor was supported mainly by two findings: (1) The positive correlation between the phenotypic diversity and the habitat diversity, which means that the more diverse the habitat, the more diverse is I. baltica in its phenotypes. (2) The inverse relation between the number of green uniformis and the amount of Fucus in the habitat, i.e. the less Fucus the higher frequency of green morphs. This relationship, as well as the reversed found (with green algae etc.), is in accordance with my results from predator-prey experiments (Korheina, paper E).

The ability of a predator to distinguish between preys may of course be a result of several factors, e.g. density of prey populations, number of predators and brightness of the colour of the prey. Prey animals that cannot blend well with their background run the risk of being rapidly eliminated. Thus, the broad varia-

bility in appearance in I. baltica may serve as an adaptation to widely structured habitats. In all localities uniformis was the most common phenotype, and the question arises if the uniform colour has any selective advantage over the other phenotypes. In my opinion the answer should be yes. Having a uniform ground colour matching the background is no doubt of great importance. On the other hand, these colour morphs are at some disadvantage, since there is a tendency for a predator to select only the common types (apostatic selection). As the isopods form an important link in the diet of many fishes, this apostatic selection could act to maintain a balanced polymorphism as the rare phenotypes are overlooked, why the selective value of each morph or phenotype tends to vary inversely with its frequency (Clarke 1962a, 1964, Cook and Miller 1977). However, at one stage or the other, by process of "learning to see" (Dawkins 1971) the predator is likely to develop a "specific searching image" for the rare phenotypes at higher densities and overlook the other phenotypes even if these are obvious (Clarke op.cit. and Murdoch and Oaten 1975).

A change in substrate is known to induce isopods, e.g. I. granulosa and I. monoyensis, to respond by slowly reversing the existing chromatophores so as to match the new substrate (Lee 1966a, b, 1967). Lee showed that the chromatophoral pigment was reduced and that the majority of pigments in Idotea were carotenoids which derived from plants (Morris 1977). It is, therefore, reasonable to suppose that these pigments are from algal food. Similar investigations of the genus Dynamene (Holdich 1969) confirmed polychromatism due to epidermal pigments derived from algae. Previous food preference experiments of I. baltica showed that green algae (Cladophora rubestris, Ulva lactuca and Enteromorpha intestinalis) and brown algae (Chroda filum and Fucus species) on which these animals clinged and fed upon, were abundant in the sampling sites. These algae are rich in B-carotene and lutein (Morris 1977). Since I. granulosa and I. baltica share similar ecological requirements, it is not far fetched to suppose that a similar mechanism of pigment production occurs in I. baltica.

The flexibility of the appearance of individual idoteas supports the hypothesis that predation is active in the evolution of phenotypes and colour morphs. On the other hand, there are examples among crustaceans where other factors than predation seem to

involved. Heath (1975) found that populations of Sphaeroma rugicauda were more polymorphic in intermediate salinities than in the extreme salinities. A similar change in S. rugicauda was correlated to temperature (West 1964).

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PREDATION ON POLYMORPHIC IDOTEA BALTICA (CRUSTACEA, ISOPODA)

BY ZOARCES VIVIPARUS (TELEOSTEI, ZOARCIDAE) -

A LABORATORY STUDY

Paper E

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Abstract

The predation of Zoarces viviparus (Teleostei) on polymorphic Idotea baltica (Crustacea, Isopoda) was studied under laboratory conditions, where algae of different colour were provided as substrate and shelter for the isopod. A differential predation was found. Thus, the proportions of the phenotypes and morphs taken by the predator seem to be influenced by the colour of the algal species present. The experiments further show that also the size of the prey was important, i.e. smaller individuals were more likely to be caught than bigger. It is postulated that in a natural population, differential predation will affect the frequency of different morphs or phenotypes differently depending on the colour composition of the algal community.

1. Introduction

In a prey population all individuals are not equally vulnerable to a predator. Besides the abundance, the availability of the prey may depend on its age, size and colour. Polymorphic species of prey are well suited for analysis of such relationships. In this respect, the isopod Idotea baltica (Crustacea, Isopoda) is particularly suitable because of its advanced colour polymorphism.

Predation on polymorphic species has been extensively studied in land snails, Cepaea nemoralis (L.) and C. hortensis (Müller) (Cain and Sheppard 1954, Goodhart 1958, Clarke 1960, Clarke and O'Donald 1964). These authors showed that the nature of the habitat influenced distribution and selection of the phenotypes.

By process of "learning to see" (Dawkins 1971) or "searching image" (Murdoch and Oaten 1975), predators select varieties frequently encountered when these have exceeded certain densities. Such apostatic selection was studied in land snails Cepaea with birds as predators (Allen and Clarke 1968, Clarke 1969, Allen 1972, Cook and Miller 1977). The results of these studies were used to explain the maintenance of colour polymorphism in the species preyed upon.

The aim of this study has been to investigate some factors affecting the predation on Idotea baltica by Zoarces viviparus. This live-bearing teleost is widely distributed along the coasts of the southern Baltic. It is abundant in the Fucus belt along the Falsterbo peninsula where most of my field work on the isopods has been carried out.

Stomach analyses have shown that Idotea species form an important link in the food chains of many fishes, e.g. the eelpout Zoarces viviparus (Sywula 1964, Lee 1966, Salemaa 1978).

2. Material and methods

The predatory effect by Zoarces on Idotea baltica was studied in the laboratory with regard to three different considerations: (1) the significance of prey colour, (2) the effect of prey size and (3) the influence of substrate on preferred prey type. For this purpose different morphs and phenotypes of I. baltica were examined. First of all the three colour morphs (green, brown and black) of the most common phenotype uniformis were tested. Besides, three other phenotypes of I. baltica common in the southern Baltic were examined e.g. albafusca, bilineata and maculata. When investigating the effect of the body size on the predation two colour morphs of the smaller species I. chelipes (Pallas) were used for comparison. In order to study the influence of the substrate (background) on prey selection some different aquatic plants, acting as a place of refuge (habitat), were tested. Besides the seed plant Ruppia spiralis, the following algal species were examined: Cladophora rupestris, Chorda filum, Enteromorpha intestinalis, Fucus vesiculosus and Ulva lactuca.

All isopods in the experiments were adults. The specimens of Zoarces were 11 to 16 cm long.

The isopods were collected from five sampling sites at the Falsterbo peninsula by shaking Fucus into a 50 x 50 cm sieve and the animals were transferred into two-liter containers, in which they were transported to the laboratory. The eelpouts were caught at the Idotea sampling sites.

An aquarium with sand bottom measuring 53 x 35 x 29 cm was filled with 50 l (10.0 %) diluted sea-water in a thermo-constant room of $12.5 \pm 0.5^{\circ}$ C supplied with two neon lights. In order to ensure that the prey was always seen in contrast with the provided background, an additional precaution was taken by surrounding the aquarium with aluminum paper to the level of the water. The water was aerated and filtered continuously but not changed during the experiment. An additional aquarium measuring 39 x 31 x 25 cm was set up for the eelpouts when awaiting to be used in the experiment. From the last mentioned aquarium one fish at a time was transferred into the main aquarium for the experiment. No one fish was used more than once per day for each algal species.

For detailed information on the morphs, see Korheina (paper D).

The algae were placed in the aquarium in order to provide refuge for the prey animals. Only one species was used at a time. Five individuals of each phenotype of I. baltica and five each of green, brown and black morphs of uniformis, a total of 30 animals were added to the aquarium at a time in the first experiment. After 30 minutes - when the isopods had hidden properly among the algae - one eelpout was gently slipped into the aquarium. After half an hour the predator was removed and the remaining specimens checked and recorded. This procedure was repeated ten times for each algal species.

In order to test the predator's reaction to preys of different size, black females of I. baltica and I. chelipes (a total of 30 animals, i.e. 15 of each species) were used as prey. In another experiment, green males of both species (also a total of 30 animals) were used as prey. The procedure was the same as above.

3. Results

3.1. Predation on isopods sitting on green algae (Chlorophyceae)

There was a bright contrast between the black morphs and the green background consisting of Enteromorpha. The contrast undoubtedly contributed to the intense predation on black individuals (33.3 %) (Tab. 1). This value was followed by 18.2 % in maculata. The least taken specimens on this alga were the green ones (9.1 %). The difference between the observed and the expected number of isopods eaten on Enteromorpha was significant ($p < 0.01$).

On Cladophora the black morph was still more preferred as a prey (35.6 %), followed by albafusca (20 %). The brown and green isopods were taken in the lowest numbers (8.9 %). The difference in mortality between the observed value and the expected was significant ($p < 0.01$).

On Ulva lactuca the brown morph of uniformis was the most preferred one (28.3 %). Surprisingly, the black idoteas were taken in the lowest numbers (11.3 %). On this algal species the difference between the observed and the expected number of animals taken was not significant.

Of all animals eaten on the green algae, 26.8 % were black morphs, followed by 17.1 % for the brown and 10.4 % for the green idoteas.

Tab. 1. Differential predation on the morphs and phenotypes of *I. baltica* on different types of substrate. Br = brown, Bl = black, Gr = green, BL = bilineata, M = maculata, AF = albafusca. * denotes $p < 0.05$, ** denotes $p < 0.01$, *** denotes $p < 0.001$, NS denotes not significant.

Algae	U n i f o r m i s				M	AF	χ^2
	Br	Bl	Gr	BL			
<u>Green algae</u>							
Enteromorpha intestinalis	eaten % eaten	9 13.6	22 33.3	6 9.1	8 12.1	12 18.2	9 13.6
Cladophora rupestris	eaten % eaten	4 8.9	16 35.6	4 8.9	5 11.1	7 15.6	9 20.0
Ulva lactuca	eaten % eaten	15 28.3	6 11.3	7 13.2	9 17.0	8 15.1	8 15.1
<u>Brown algae</u>							
Chorda filum	eaten % eaten	11 14.7	11 14.7	20 26.7	13 17.3	17 22.7	3 4.0
Fucus vesiculosus	eaten % eaten	2 3.6	13 23.2	18 32.1	9 16.1	8 14.3	6 10.7
<u>Green and yellow seedplant</u>							
Ruppia spiralis	eaten % eaten	10 20.0	7 14.0	10 20.0	7 14.0	9 18.0	7 14.0
Total % prey eaten		14.8	21.7	18.8	14.8	17.7	12.2

3.2. Predation on isopods sitting on brown algae (Phaeophyceae)

With brown algae as the background, the contrast between the green morph and the algae was very pronounced. As a result of this contrast, the specimens of green morph were incapable of concealment and their mortality was high. The mortality of the green morph was 26.7 % and of maculata 22.7 % when they occurred on Chorda. Only 4 % of albafusca were eaten. On the Fucus vegetation, the heaviest predation (32.1 %) was on the green morph, followed by the black morph (23.2 %) and least (3.6 %) on the brown morph. The difference between the observed and the expected number of isopods selected on Fucus was significant ($p < 0.05$).

Of the isopods eaten on the brown algae, 29.0 % were of green morphs, 19.1 % of maculata and 9.9 % of the brown morphs. The prey selection on the brown algae was significant ($p < 0.001$).

3.3. Predation on isopods sitting on a seed plant (Ruppia spiralis)

With light yellow stem and green leaves in Ruppia spiralis, brown and green morphs were eaten in equal proportions (20.0 %) followed by maculata (18.0 %) and black uniformis, bilineata and albafusca (each 14.0 %). The difference between the observed and the expected prey selection on Ruppia was not significant ($p > 0.1$).

3.4. The influence of prey size on predation

When two different size classes of black prey (females) were used in the experiments, the smaller I. chelipes (mean 8.2 mm) was more frequently taken than the larger I. baltica (10.0 mm) (Tab. 2). This was significant in Ulva ($p < 0.01$), Fucus ($p < 0.01$) and Ruppia ($p < 0.05$).

In another experiment green males of I. chelipes (mean 10.4 mm) and of I. baltica (mean 13.5 mm) were tested as prey items (Tab. 3). The number of specimens taken by Zoarces was less on Chlorophyceae than on Phaeophyceae. Predation was furthermore heavier on the smaller I. chelipes than on I. baltica (significant for Cladophora; $p < 0.05$).

These results show that the smaller isopods were always taken more frequently than the larger ones, irrespective of plant species, sex or colour morph of the isopods and the prey selection of Zoarces was significant in some species combinations.

Tab. 2. Differential predation on black females of I. chelipes (mean 8.2 mm) and I. baltica (mean 10.0 mm) on different substrate. For significant levels, see Tab. 1.

Substrate		eaten	not eaten	% eaten	χ^2
<u>Green algae</u>					
Enteromorpha intestinalis	I.baltica	49	101	32.7	1.74 ^{NS}
	I.chelipes	61	89	40.7	
Cladophora rupestris	I.baltica	52	98	34.7	3.13 ^{NS}
	I.chelipes	68	82	45.3	
Ulva lactuca	I.baltica	41	109	27.3	7.72**
	I.chelipes	65	85	43.3	
<u>Brown algae</u>					
Chorda filum	I.baltica	38	112	25.3	2.68 ^{NS}
	I.chelipes	52	98	34.7	
Fucus vesiculosus	I.baltica	40	110	26.7	6.65**
	I.chelipes	62	88	41.3	
<u>Green and yellow seedplant</u>					
Ruppia spiralis	I.baltica	58	92	38.7	4.86*
	I.chelipes	78	72	52.0	

Tab. 3. Differential predation on green males of I. chelipes (mean 10.4 mm) and I. baltica (mean 13.5 mm) on different substrate. For significant levels, see Tab. 1.

Substrate		eaten	not eaten	% eaten	χ^2
<u>Green algae</u>					
Enteromorpha	I.baltica	6	144	4.0	0.67 ^{NS}
intestinalis	I.chelipes	8	142	5.6	
Cladophora	I.baltica	4	146	2.7	5.35*
rupestris	I.chelipes	12	138	8.0	
Ulva	I.baltica	7	143	4.7	0.53 ^{NS}
lactuca	I.chelipes	11	139	7.3	
<u>Brown algae</u>					
Chorda	I.baltica	15	135	10.0	1.48 ^{NS}
filum	I.chelipes	23	127	15.3	
Fucus	I.baltica	18	132	12.0	1.67 ^{NS}
vesiculosus	I.chelipes	27	123	18.0	
<u>Green and yellow seedplant</u>					
Ruppia	I.baltica	10	140	6.7	3.82~*
spiralis	I.chelipes	19	131	12.7	

4. Discussion

Due to the natural selection, and as long as the reproductive success of a predator is food related, the strategy must be to harvest the food resources in an efficient way. A predator not only has to decide what to eat but also when, where and how. In my experiments it was shown that the colour of the prey influenced the food choice of the predator, indicating that Zoarces viviparus is a typical "by sight" hunter. On the other hand, the colour in itself was of no crucial importance for the selection as all three colour morphs of uniformis were preyed upon. Instead, the selective predation may be related to the nature of the background (algal species). The colour of the Idotea morphs which matched their background (e.g. green isopods on green algae) were selected in less numbers than those which did not blend so harmoniously with the surroundings. In all experiments, when all three colour morphs of uniformis as well as the three other phenotypes of I. baltica were simultaneously tested, always one of the colour morphs of uniformis was most heavily preyed upon and in all but one experiment, one was the least taken. Thus, the three other phenotypes of I. baltica were intermediate in this respect. Their spotted appearance, in contrast to uniformis, gave them about equal chance in almost all substrates, which may serve as an adaptation to widely structured and diverse habitats.

The broad variability of the colour pattern in I. baltica may be seen as a strategy to circumvent predation; the force probably driving the evolution and maintainance of such a variation. The greatly varying appearance also gives another advantage to the prey, namely by rendering the "learning process" or specific "searching image" of the predator inefficient (cf. Clarke 1969, Dawkins 1971, Murdoch and Oaten 1975).

The experiments revealed that the fishes were capable of discriminating between objects not only according to colour but also to size. Thus, the size of the prey was found to greatly affect the choice, i.e. the smaller idoteas were preferred to the larger ones. The reasons for the avoidance of the larger prey are not known, but selection may have been influenced by factors governing searching or handling the prey. It is reasonable to believe that the choice is also related to the size of the predator, i.e. larger specimens of Zoarces would have taken larger prey items. On the other hand, mobility is another important factor in the predator-prey relationship. It can be argued that the differential mor-

talities of the Idotea species, under the attack of a predator, might to some part have been due to a different activity of the Idotea individuals. The Idotea species are rather slow moving animals and so far no differences in moving or speed between the two groups compared, were observed.

In a natural population differential predation might be more pronounced during some periods than others. Thus, the drastic reduction of large males during the summer months may to some extent be due to the sex-related size difference, which possibly makes the male isopod a more attractive prey than the female.

The present experiments further implies differential predation to be important for the frequency of phenotypes and morphs occurring in a natural population. Thus, in the southern Baltic differently coloured algae dominate in different areas. It is reasonable to believe that in these areas selective predators will tend to eliminate those morphs and phenotypes of Idotea which do not blend with the background.

5. References

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